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to the foraging behaviour**

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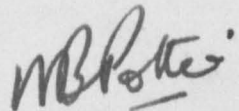
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Memorandum on a thesis for the degree of Ph.D.

By

N.B. Potter

This dissertation is based on my own independent work,
carried out under the supervision of Dr. H.E. Hinton in the
Department of Zoology in the University of Bristol, in the years
1960 - 1964.



N.B. Potter

Dissertation for the Degree of Ph. D.

A STUDY OF THE BIOLOGY OF THE COMMON WASP, VESPULA VULGARIS L.,
WITH SPECIAL REFERENCE TO THE FORAGING BEHAVIOUR.

By

N.B. POTTER

Department of Zoology

University of Bristol.

March, 1964.

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I INTRODUCTION

The biology of the genus Vespula has not been studied very fully in recent years. This is probably due to the natural hazards of working with large colonies of these insects, and the fact that the season in which observations can be made is of such short duration - the nest history usually being completed in about five months.

In the later half of the last century and around the turn of the century, several authors made observations on the general nest cycle and described the behaviour of the adults. Ormerod (1868), Janet (1903) and DuBuysson (1903) confine themselves entirely to the simple but detailed description of the behaviour of wasps. Weyrauch (1935) made a thorough and detailed investigation of the structure and biology of wasps' nests and made some observations upon the productivity of nests by observing the number of queens produced in nests of different sizes. Duncan (1939) reviews the literature on the genus Vespula and describes the morphology of the adult. Richards (1953) gives a good general description of the history of a wasp nest. Gaul (1950 - 1954) has written a series of descriptions of the different types of behaviour exhibited by various species of Vespula. The only detailed study of the nest biology of a species of Vespula was carried out by Brian and Brian (1952) on V. sylvestris. Their observations were, however, limited by the fact that the colony died out after the production of a few workers.

The most illuminating work on the behaviour of the social Vespidae

has been performed on species of Polistes, which have a small colony size and do not cover their nests with envelopes, so obscuring the behaviour of the workers from the observer. Deleurance (1948) has shown that caste determination is dependent upon the age of the colony and that worker egg laying is inhibited by the queen. Pardi (1946) described the founding of nests of Polistes in northern Italy by more than one queen. One of the original queens in each nest becomes the dominant individual and lays eggs; the ovaries of the other queens then regress, and they act as workers. In this present work, the aim has been to study the basic pattern of population growth in nests of Vespula vulgaris L. and to link this with the behaviour of the workers. The ways in which the internal nest conditions are expressed by the foraging behaviour of the workers were also investigated. The returning foragers were first caught in a net and transferred to small boxes or sucked into a pooter. When all the foragers had been caught, it was possible to excavate the nest by digging down the entrance hole until the nest was uncovered. The teneral adults could then be collected from the outside of the nest with a pooter. They left the nest and usually ran around on the envelope. The nest was then carefully cut away from its suspension and re-housed in one of the special observation boxes.

Later in the season, when it was necessary to collect larger nests, this was done at night and an anaesthetic was used. Ether, chloroform, and trichloroethylene were tried. Ether was found to be the most reliable

II MATERIALS AND METHODS

a) Finding and collecting nests

Observations were made on Vespula vulgaris L. As queens in captivity could not be induced to start nests, nests were collected in the field. Small nests were found by two methods:

- i) The flight lines of wasps leaving posts, where they were collecting pulp for nest construction, were noted.
- ii) The vegetation along banks and other likely nesting sites was brushed. This disarranged the vegetation and the returning workers were unable to find the nest entrance. The approximate location of the nest was thus easily spotted.

In the early part of the season, when nests consist of a queen and not more than a dozen workers, it was possible to collect the nests during the day. The returning foragers were first caught in a net and transferred to small boxes or sucked into a pooter. When all the foragers had been caught, it was possible to excavate the nest by digging down the entrance hole until the nest was uncovered. The teneral adults could then be collected from the outside of the nest with a pooter. They left the nest and usually ran around on the envelope. The nest was then carefully cut away from its suspension and re-housed in one of the special observation boxes.

Later in the season, when it was necessary to collect larger nests, this was done at night and an anaesthetic was used. Ether, chloroform, and trichlorethylene were tried. Ether was found to be the most satis-

factory of these and the easiest to use. A plug of cotton wool soaked in ether was placed over the entrance hole and after a short time the nest was excavated and transported to the laboratory.

b) Nest Boxes

Nests were originally put in simple boxes with glass bottoms. The height of the comb above the glass was adjusted by a threaded rod and wheel. This system provided too little insulation which resulted in a greater fluctuation in nest temperature than was desirable.

A more elaborate type of nest box was therefore developed. This was constructed of $\frac{5}{8}$ inch block board, and was so designed that an insulating air layer one inch thick surrounded the nest chamber. The door of the inner chamber was made of one-eighth inch perspex to enable observations to be made from the side of the nest. (Figs. 1 and 2).

In the course of experimentation, it became desirable to be able to regulate the temperature and humidity of the nest. Consequently, for certain experiments, a perspex box was built incorporating a water jacket, the temperature of which was controlled thermostatically by a heater unit. The water in the jacket and the air in the nest chamber were circulated by motor driven propellers. (Figs. 3 and 4).

c) Entrance tubes

When the nests were first installed in the nesting boxes, a simple perspex tube was used as an entrance passage. This was left in position until the wasps had thoroughly settled down. The simple tube was then replaced on occasions by a more complex type (Figs. 5 and 6). This was

designed to separate the wasps entering from those leaving the nest, so that exits and entrances could be counted automatically by means of a double circuit photoelectric counter (Figs. 5 and 6). It will be seen from the figure that the passages to and from the nest were tapered, so that wasps moving in either direction entered the wide end and emerged from the narrow end. Each circuit of the counter consisted of a photo-sensitive transistor Mullard (0:C:P. 71) and diode (0.A.81), a relay, a "Post Office counter" and a $4.7\text{ K } \Omega$ resistance (Fig.7). The 48 v. battery was obtained by using the correct terminals of a 120 v. Exide dry battery H. 1006 and the 24 v. by joining 5 Exide $4\frac{1}{2}$ v. batteries H. 30 in series. Wasps walking along the tube in the direction of the arrows interrupted the light beam from the bulb in the bulb holder (7) illuminating the phototransistor. The pulse so obtained was recorded electrically on the Post Office counter.

The accuracy of the counter was tested at intervals throughout the season. It was found to be more accurate when used on smaller nests. When used on larger nests, it was sometimes found that the foragers leaving the nest were so close together that there was no appreciable gap between two consecutive wasps, which therefore did not record separate pulses. This also applied to wasps entering the nest. It was found that the entrance counter was always more accurate than the exit counter. This was because the guard wasps, which always used the exit tube, sometimes walked up and down in it, or stood in the beam, so interrupting the circuit. The counting errors were never found to be

more than 5% in the entrance counter or 20% in the exit counter. The lowest figures for accuracy were always found in the evening, when the foraging activity of the wasps was declining, and the incidence of guard wasps was increasing.

d) Marking wasps

Wasps were marked by means of coloured cellulose paints. Five colours were used - red, yellow, orange, white, and green. These colours were put on the wasps in three positions : anterior thorax, posterior thorax, and on the first abdominal segment. This gave more colour combinations than it was possible to use at any one time.

e) Age of wasps and time analysis of foraging activities

As soon as possible after they had emerged, young teneral adults were removed from the nest, marked, and returned to the nest. Observations were made during daily two-hour periods, the periods of 10 - 12 a.m. and 3 - 5 p.m. being used alternately, and it was noted at what age the wasps first started to forage, what substances they collected, and how long each foraging trip lasted. The exits and entrances of the marked wasps were recorded on a transistorised tape recorder, together with a note of their foraging activity (i.e. whether they were bringing back pulp, insect flesh, or fluid). After the two hour sampling period, the recording was played back while a stop watch was running, and the time of the exit and entrance of each marked wasp was noted. It was then possible to calculate the duration of the activities of individual wasps, and the frequency of these activities during the two hour sampling period.

III INTRODUCTION TO THE STUDY OF INDIVIDUAL NESTS

Before the detailed analyses of the activities of wasps in individual nests are compared, the stages through which all successful nests pass will be considered. Many nests were taken and their worker population, foraging rate (i.e. trips per hour), number of cells and brood recorded. (Appendix 1 and 2). These figures led to the build up of a general picture of nest development and population growth. (Fig.8).

From the graphs constructed from the figures recorded in the appendix tables 1 and 2 it is possible to divide the life history of the wasp colony into five stages. The duration of each stage, and the time of the year at which it occurs, obviously vary widely, depending upon the individual nest and the weather conditions. Fig.8 represents a normal nest in an average year.

The five stages can be briefly described as follows:-

- STAGE I Solitary stage The queen builds the nest, provisions the cells, and rears the first brood of workers.
- STAGE II Rapid increase The workers replace the queen as the foraging force. The queen is now a nurse and egg producer. There is a very rapid build up of worker population. The foraging rate per worker is high and the worker/larva ratio low.
- STAGE III Slow increase The rate of population growth is not so rapid as in stage II. The foraging rate per worker is much lower and the worker/larva ratio higher.

STAGE IV Climax of colony The worker population is not increasing. The cells being built are all queen cells. Males emerge, and the worker/larva ratio drops, and the foraging rate per worker increases.

STAGE V Decline The decline is probably caused by the death or sickness of the queen. The colony cohesion breaks down, cannibalism sets in, and the foraging becomes erratic.

Fig.9 shows the changes in the worker/larva ratio throughout the different stages, and Fig.10 the rate of worker and queen cell construction. By plotting the total foraging rate of workers in the nests against worker population (graph Fig.11), it is seen that, during the early stages of colony development, the foraging rate increases nearly as rapidly as the number of workers increases (stage II). As the nest grows and enters stage III, however, the foraging rate increases more slowly and no longer keeps pace with the rate of population growth. In stage IV, when queens are reared in the nest, the worker population begins to decrease and foraging rate increases until it reaches a rate comparable to that of stage II.

Only data obtained from nests which had not yet built any queen cells (stages II and III) were used in compiling graph Fig.12, as the effect of the presence of queen larvae was not known. It will be seen (Fig.12) that a plot of the foraging rate against the number of larvae gives a straight line, and therefore foraging rate is directly proportional to the number of larvae throughout stages II and III. It has

already been seen that the ratio of the foraging rate to the number of workers declines from stage II to stage III. This means that the workers are not foraging as fast as they could in stage III, and so it can be concluded that some other factor is determining the rate of growth of the nest population in this stage. The limiting factor could be the maximum rate at which the queen is able to lay eggs.

If this assumption is correct, the maximum number of eggs laid per day can be approximately calculated, by dividing the number of brood (larvae plus cocoons) during the latter part of stage III, when the nest population is approximately constant, by the stage III generation time. From measurements in several nests, the number of brood in stage III has been determined as approximately 6 - 8,000, and the generation time as approximately 24 days. It is thus deduced that queens lay a maximum of 200 - 300 eggs per day.

IV THE BIOLOGY OF THE NEST

a) STAGE I, the solitary stage

1) General

When the queens come out of hibernation in the spring they spend some time feeding at the flowers of shrubs, (Cotoneaster, Berberis, etc.). Soon they start looking for a suitable nesting site. When searching for a suitable site they fly with a slow, swinging flight low over the ground. While doing this they settle on any round, dark object or depression in the ground and examine it. If it is a hole, they walk in and spend a varying time examining the site, moving on if it is not suitable. It is not clear exactly what governs the choice of a site for nest building, as nests are found in very different types of situation. The physiological state of the queen is possibly a most important factor determining the time and place of nest initiation. When the 'nest building drive' is sufficiently strong the queen will possibly choose the first suitable nesting site.

Having discovered a suitable nest site, the queen backs out of the chosen hole and commences a thorough orientation flight. The queen orientates in a way similar to that of the workers (Gaul, 1950). She flies backwards and forwards in front of the nest site entrance with a slow, hovering flight. This is repeated, with the distance from the site increasing slowly. When the arc of flight has increased to about 6 feet, the flight path becomes a figure of eight of ever increasing size. When the queen is about 60 feet from the nest site she flies

away in a straight line. By this type of flight she fixes the position of the nest relative to certain landmarks in the immediate vicinity of the nest.

The queen now begins to build the nest. Most of the information on nest construction in the Vespinae is based on evidence from fairly advanced nests and from those rebuilt by the workers after their nests had been destroyed (Janet 1903). Duncan (1939) states that there are conflicting reports about the initial construction of queen nests. A detailed description of two nests of Vespula sylvestris Scop. is given by Brian and Brian (1948).

The writer only once observed the initial stages of nest construction, at Failand in June 1961. Several queens were seen examining the banks of the road for nesting sites, where artificial sites had been prepared by digging small hollows, laying sticks across the tops and then covering the whole with flat stones, leaving a small gap to act as an entrance hole. A Vespula vulgaris L. queen was seen entering one of these artificially prepared nesting sites with a load of pulp on June 6th. When the queen had left, the stones were removed and the initial stage of the nest was found. It then consisted of a small knob of paper attached to the under side of the stick (Fig.13). One of the stones was left off the top of the nest hole to allow observations to be made. The queen was not disturbed by the light, and once she had entered the nest chamber, she immediately commenced to add pulp to the nest attachment to form the spindle. When attaching the

pulp, the queen clung to the stick with her two posterior pairs of legs, while she worked the pulp with her anterior legs and mouth parts, attaching it to the centre of the suspension sheet (Fig.14). The next load of pulp was attached in a similar manner, the queen working round the spindle as she applied the pulp. The following four loads were applied by the queen while clinging to the spindle rather than to the stick. These loads completed the formation of the spindle.

The next load of pulp was added to the end of the spindle, but it was worked into a small cup (Fig.15). The next pulp load was added to this first cell. The queen then commenced the second cell below and on the side of the first cell, unlike V. sylvestris Scop. which, on the two occasions observed by Brian, made its second cell above the initial cell (Brian and Brian, 1952).

Work was then begun on the first envelope. When constructing the original part of the envelope the queen clung to the spindle with her body curled around it and her legs resting on the top of the cells. This gave the characteristic distance of approximately 5 mm. between envelope and cells (Fig.16). The queen worked backwards around the spindle until she had completed the circuit, thus forming the collar. The next load was similarly applied to the edge of this collar and succeeding loads were applied while the queen stood astride the envelope edge.

After the second load of pulp had been applied to the envelope, the queen always adopted the same procedure when building. Her behaviour

was like that described by Duncan (1939) for workers and by Brian and Brian (1952) for queens. On returning to the nest, the queen always alighted on the envelope and then crawled into the nest, where she sat on the cells and cleaned her wings, antennae, and legs. She then applied the load of pulp. If this was to be applied to the envelope, the queen would walk around the envelope examining its edge with her antennae. When she had selected the position to which the paper was to be attached, she applied the paper with her mandibles in a strip to the edge of the envelope, while she walked slowly backwards on her posterior pair of legs. The anterior pair of legs was used to guide the ball of pulp. When the whole load had been applied, the queen ran forwards to the end of the newly laid strip and began to thin the strip by ventro-dorsal pulling and biting movements of the jaws. This thinning was usually repeated twice, after which the queen entered the nest and took up her resting position around the spindle, between comb and envelope.

Two days after the nest was begun (Fig.17), it was moved into the laboratory, where it was placed in an observation box. The next morning the queen was seen working steadily on the nest. By mid-day on the third day, the first envelope was complete and the second envelope had been started. At this stage six cells had been built, five of which contained eggs (Fig.18). (Eggs are usually laid as soon as a cell initial is complete).

The following stages of nest development can best be shown by

diagrams and corresponding cell maps (Fig. 18, 19 and 20).

2) Activity of the queen

At first, the queen worked only at nest construction. This entailed only one type of foraging, the collection of pulp. It was apparent from the two different colours of paper applied to the nest that the queen was collecting pulp from two different sources, A and B. The length of time taken collecting pulp from source A was 6 min. \pm 15 sec., whereas the time for collecting from source B was 8 min. \pm 1 min. 7 sec. The difference in the time taken to collect a load of pulp from the two sources might have been due to two factors : the sources being at different distances from the nest, or source A being more easily worked than source B.

During the first five days of nest construction the queen foraged only for pulp, and her activity was divided between pulp collection, building, and resting in the nest in her characteristic position, curled around the spindle. During the succeeding days there was a progressive change in the foraging activity of the queen. This was partly related to the cell contents. On day six, larvae hatched in cells 1 and 2, and on day 7 one hatched in cell 3. When larvae hatched, a change in foraging was necessary in order that the larvae might be fed. The queen now started to forage for fluids and a little insect flesh; pulp was, however, still collected as cells were still being built.

The activity of the queen before the workers began foraging was observed daily for a two hour period - the periods of 10 to 12 a.m. and

Table I. 10-12 A.M.

Day	6	8	10	12	14	16	18	20	22	24
Pulp	5	5	3	1	—	—	—	—	—	1
Fluid	2	3	4	5	4	5	6	4	3	3
Insect	—	—	1	2	2	1	—	1	1	—

Table II. 3-5 P.M.

Day	7	9	11	13	15	17	19	21	23	25
Pulp	7	5	1	1	—	—	1	—	—	—
Fluid	—	3	6	5	4	6	4	4	2	1
Insect	—	1	2	2	3	1	3	—	1	—

3 to 5 p.m. being used on alternate days. Tables I and II show the results of these observations. It can be seen that the queen collected a large amount of pulp in the initial stages of nest construction, and that this was later replaced to a large extent by foraging for fluid and insect meat. Pulp collection did not stop completely, but continued at a low rate until the workers replaced the queen as the foraging force. The decrease in pulp collection was probably due to the increased larval demand for food - fluid and insect flesh. These activities appeared to occupy all the queen's time. As was noted by Brian and Brian (1952), fluid is an important part of the diet of wasp larvae. During the observation periods of days 6 to 25, fluid collection took precedence over insect flesh collection - 73 loads as compared with 21 loads. There was a tendency for more fluid to be collected in the morning (10 to 12 a.m.) when the ratio was 38 : 8 than in the evening, when it was 35 : 13. Insects were sought more in the evenings than in the morning. This tendency towards morning fluid collection and evening insect collection was noted by Brian and Brian (1952) for workers of Vespula sylvestris.

The amount of insect flesh collected was large during days 11 to 19. This was the period during which there were most larvae in the inward facing stage (instars 4 to 5). After the first batch of larvae had spun cocoons (which they had completed by day 24), the amount of insect flesh collected decreased and finally ceased. After day 23 no insect flesh was seen to be brought into the nest, and the only activity

of the queen after this stage was foraging for fluid and nursing the brood. After day 22, when the first seven larvae had spun cocoons, the queen's activity was reduced to an occasional sortie for fluid. This situation continued until the first workers commenced foraging on day 25. A cessation of the queen's foraging activity at this stage is probably of general occurrence. It was noted in V. sylvestris by Brian and Brian (1952). Larvae are starved in this period, and their developmental period is thus prolonged (cells 10 to 16 in this particular nest). Fig 34.

The eggs laid by the queen on any newly constructed comb are always attached to that corner of the hexagonal cell which is nearest to the central axis of the comb. This orientation of the egg is due to the fact that the queen lays an egg in each cell very soon after its initiation. The queen stands on the comb and lays the egg in the nearest corner of the cell; this is the only corner of the cell which is completed at this stage. Eggs laid in a complete cell after it has been vacated by an emerging adult are usually fixed to one of the angles nearest to the centre of the comb. Eggs laid in cells which have been used are always placed about half-way down the cell. When ovipositing in old cells, the queen inserts her abdomen as far into the cell as possible. She then moves on the surrounding cells until she finds one of the angles of the cell to which she attaches the egg. The slight curvature of the cells causes the queen to align herself preferentially along the radius of the comb. This results in the characteristic orientation of the eggs.

3) The brood

From the brood sequence shown in the cell chart (table 34) the following observations can be made :

Eggs

Brian and Brian (1952) found that the incubation period for about the first ten eggs laid by a Vespula sylvestris queen was five days. However, they found that the apparent incubation period of later eggs was up to fifteen days. They put forward three possible explanations of this apparent increase in incubation period : changing physiological or climatic factors, cannibalism and immediate replacement, and the low viability of eggs combined with efficient scavenging and replacement. Cannibalism might have been due to hunger caused by a reluctance to forage because of bad weather or the maturation of the queen.

The incubation period of Vespula vulgaris was found to be five days as in Vespula sylvestris. There was some evidence of a slight lengthening of the incubation period, but, except in the cells (4, 22, and possibly 17) where cannibalism or scavenging and replacement were observed, the longest incubation period was seven days. This observed increase in incubation period could have been an artifact produced by the method of sampling every 24 hours, with the eggs laid just before sampling and hatching soon after it. The frequency with which varying incubation periods occurred is shown below:

TABLE III showing the length of incubation of eggs

Days incubation	No. of cells
5	15 (cell 4 and 22 after replacement)
6	5
7	2
8	?1 (cell 17)
	—
	23
	—

The queen, during her initial bout of egg laying, (Stage I, days 1-15) laid 25-26 eggs.

It is apparent that the majority of eggs hatched within five or six days. From the evidence of this nest, although of a different species to that considered by Brian and Brian (1952), it seems probable that the apparent prolongation of incubation period they observed was due either to cannibalism or low viability and consequent scavenging and replacement rather than to a physiological cause.

Larvae

The details of larval development in the Vespidae have given rise to some controversy. Ormerod (1868) believed that there were only two larval instars, DuBuysson (1903) three, and Yoshikawa (1962) claimed that there were four. Brian and Brian (1952) divided the larval period of Vespula sylvestris into two stages for recording details of colony development - an initial, fixed, outward facing stage and a free-moving,

inward facing stage - but made no attempt to distinguish the larval instars. the larval period is short, but if for some reason the supply

Observations of the changes in mandibular size and shape (Figs. 21-25) made by the writer on V. vulgaris showed that there are five larval instars of which the first three are fixed, facing outwards away from the axis of the comb. (Outward facing stage of Brian). These instars (Figs. 26, 27 and 28) remain fixed with their abdomens within the split egg shell. The cement by which the queen attaches the egg to the side of the cell thus acts as the point of attachment for the first three larval instars. The larvae hold themselves onto the egg shell by means of a viscid secretion (Du Buysson, 1903).

After the ecdysis to the fourth larval instar, the larvae become free to move in their cells, and now hold their position in the cells by means of their pleural lobes and dorsal ridges (Figs. 29 and 30). The larvae now re-orientate themselves, and they rotate through 180° from the fixed, outward facing position of the earlier instars, to face inwards towards the axis of the comb. The early fifth instar larva is very similar to the fourth instar, but during this final instar the larvae grow very rapidly and come to fill the cell completely. The dorsal ridges and pleural lobes become less obvious and the larvae become more rounded and less annulated in appearance (Figs. 31 and 32).

The duration of each larval instar and of the whole larval period vary considerably. The larval period and the duration of each individual instar, is dependent upon the trophic condition inside and

outside the nest. If large quantities of food are being brought into the nest, the larval period is short, but if for some reason the supply is small (because of bad weather and poor foraging conditions, or a drop in the foraging activity for physiological reasons) the larval period is extended. This variation in larval period is especially marked during the period of nest initiation when only the queen is foraging, because, as has been seen in the previous section, the queen only forages for a limited period.

In the nest described at the beginning of this section, the fixed, outward facing stage (instars one, two and three) was sometimes as short as three days, but four to five days was the more usual duration. During the period in which the queen's foraging activity decreased, and before the workers commenced foraging, the period was increased up to eleven days. The inward facing period (instars four and five), during which most growth takes place, lasted six to seven days. This was longer than the three day period noted by Brian and Brian (1952) for V. sylvestris cells 1-4. During the period of reduced foraging by the queen, after the first nine cocoons were formed, the duration of the inward facing stage was increased up to sixteen days (cells 11 and 12).

During a prolonged spell of bad weather in August, 1963, the larval period of Vespula vulgaris in a large nest (in stage III) kept constantly at 32°C. in the laboratory was extended from the usual nine days up to seventeen days.

The generation time of V. vulgaris varies with the foraging

conditions outside the nest. This variation is more noticeable during stages II and IV, when the number of workers and their foraging rate are limiting the rate of population growth, than in stage III, when some other factor is limiting the population growth (possibly the egg laying capacity of the queen, as discussed previously). In times of poor foraging conditions, more foragers can be recruited during stage III to maintain a constant trophic condition within the nest. In stages II and IV, there is little foraging potential that is not utilised, and therefore poor foraging conditions result in the starvation of the larvae and a consequent prolongation of the larval period. In stage III the generation time is usually 23 - 25 days, but in stage II it can be as long as 35 days when foraging conditions are poor.

Cocoon formation and pupae

When fully grown, the final larval instar commences to spin a silken cocoon. The larva rotates its head round and round, attaching the silk to the edge of the cell. When there is a fringe of silk around the cell the larva works in towards the centre of the cell until the top is completely closed. In order to explain the presence of the silken cocoon at the bottom and sides of the cell, Ormerod (1868) stated that the larva spun its cocoon continuously from the time it became free to move in the cell. If this were the case, the salivary glands from which the silk is secreted would be double structures, producing both silk and saliva continuously. In fact, once the larva has completed the cap to the cell, it inverts itself so that its head is at the bottom of the cell.

When it has done this it spins the bottom portion of the cocoon. How the larva performs this feat in a closely fitting cell is difficult to imagine. Larvae were, however, found in this inverted position in all examined combs containing many capped cells. Occasionally a meconium is found in the silken cap of the cell, showing that the larva was inverted at the time of its excretion.

As soon as the cocoon is completed the larva returns to its original orientation within the cell, facing inwards towards the axis of the comb. It now voids its meconium. The meconium consists of all the indigestible substances which the larva has been fed in its life, and which have been stored in the blind mid-gut. The main constituent of the meconium is small pieces of insect cuticle.

After the excretion of the meconium, the larva begins to change its external appearance; the pupal thorax becomes demarked and it can be seen that it is at this stage that the first abdominal segment is incorporated in the thorax, Fig.32.

The capped cell stage is of variable duration, as noted by Brian and Brian (1952) for V. sylvestris. The later-formed cocoons, 10 - 23, persisted for longer than the earlier-formed cocoons 1 - 9. The cocoons in cells 1 - 9 averaged 8 days from spinning to the emergence of the adult; those in cells 10 - 23 averaged 14 days. This lengthening of the period within the cocoon cannot be explained by climatic conditions. The longer the larval period, the longer is the period within the cocoon.

The pupal period of 7 - 22 days mentioned by Brian and Brian (1952)

for V. sylvestris is, in fact, made up of several stages which are hidden by the cocoon. After the completion of the cocoon, three days elapse before the larval-pupal ecdysis. The wasp hatches from the pupa but remains within the cell for two to three days before starting to eat its way out. The cocoon period thus consists of the following stages:- 5th larval instar, pharate pupa, (Fig.33), pupa, pharate adult, adult. The true pupal stage is thus of quite short duration; about three days, from the larval-pupal ecdysis to the pupal-adult ecdysis.

Adults

The first adult emerged on the 23rd day and the emergence of the queen-pupated brood was complete by the 33rd day. Adults emerged from the cells by cutting away the cap of the cell from the inside, using their mandibles. They effected their own release unaided by the queen or other workers. Once the adult had left the cell other workers removed the ragged parts of the cocoon from the cell edge.

The first brood of workers were of normal size, as they were in V. sylvestris (Brian and Brian, 1952). The next generation of workers, those emerging from cells 10 - 23, were, however, diminutive. These larvae had suffered a prolongation of larval period due to starvation when, after the pupation of the first batch of brood, cells 1 - 9, the queen's foraging activity was reduced. The average weight of the first 9 workers was 127 mgrms., but the workers from cells 10 - 23 averaged only 82 mgrms. The next generation of workers, entirely reared by

workers, were of the same size as the first queen - reared workers, or even a little larger - 132 mgrms. being the average weight of 10.

The workers began foraging on the second or third day after emerging. For the first few days pulp collection predominated but this soon gave way to a mixture of all types of activity. The first insects were seen to be brought in on the third day of foraging.

Note:-

Owing to an accident during the anaesthetising of the next, in order to mark the workers, the queen was killed, and so observations were discontinued and the following records were made on a different nest at a similar stage of development.

b) STAGE II, Stage of rapid increase

In this stage the workers have replaced the queen as the foraging force and the queen is concerned only with nursing and egg production. As her ovaries develop, her abdomen becomes distended with eggs and she loses the ability to fly. The workers forage hard with only short rests between flights. The ratio of larvae/workers is high and the ratio of the foraging rate (trips per hour)/number of workers is also high. The generation time from egg to adult is now similar to that observed in the first cells, 1 - 4. The workers begin to forage on the second to fourth day after emergence and attain a maximum foraging rate five to fourteen days after emergence. During these nine days their foraging activity is constantly high. After the seventeenth day, their foraging activity declines and the length of time spent on a foraging trip increases.

STAGE II, The effect of ageing on the foraging of workers

The length of life of the workers of Vespula vulgaris L. is shown by the histogram in Fig. 35. The average length of life was fourteen days during this period, although some wasps lived for 27 days.

When considering the effect of ageing on the foraging activities of workers, it was necessary to introduce the concept of the standard trip. This compensated for the ontogenetic changes in the type of foraging. As a worker ages it collects less pulp and more fluid, and since fluid collection takes longer than pulp or insect flesh collection, the need for the concept of a standard trip is evident.

On any one day, the standard trip (or the average duration of a foraging trip) was calculated by taking the sum of the average duration of a trip for pulp, a trip for fluid, and a trip for insect flesh, and dividing it by three. These figures were calculated from observations made on a certain sample of workers, initially numbering fifty. The number of workers in the sample decreased as workers died.

The average total foraging time per worker in the sample period is the total time spent foraging by the whole sample of workers, divided by the number of workers in the sample.

The number of standard trips made by the sample of workers on the day in question is the average total foraging time per worker, divided by the average duration of a foraging trip.

AVERAGE DURATION OF		Sum of the average times spent
A FORAGING TRIP	=	collecting pulp, fluid, and
(The standard trip)		<u>insect flesh on the day in question</u>

3

AVERAGE TOTAL FORAGING TIME PER WORKER IN SAMPLE PERIOD	=	Total time spent foraging by the whole sample of workers no. of workers in sample
NUMBER OF STANDARD TRIPS	=	<u>Average foraging time per worker</u> Average duration of foraging trip

The graph, Fig.36, shows the number of standard trips completed during the two hour sample period ~~at~~ progressive stages throughout the life of the sample of workers. Observations on any day during which the weather conditions were other than fine were not considered. Poor foraging because of rain in the middle of the day, and subsequent foraging for water, would affect the average duration of a foraging trip and so bias the results. From the graph it is evident that the number of standard trips carried out during the sample period decreases as the workers age. This might be due to one of two factors:-

- i) The speed of foraging might decrease as the worker aged.
- ii) The wasps might spend progressively longer in the nest between foraging trips as they aged.

Graph Fig.37 shows the average duration of foraging trips plotted against the age of the wasp. From this, it can be seen that the older wasps do, in fact, take longer to collect a load when foraging. This could be because they collect larger loads. However, the size of a load of insect flesh varies considerably irrespective of the time taken to collect it, or the age of the worker. Aged wasps often spend very much longer collecting fluid than they did when young, and obviously do not

collect proportionately more fluid. Therefore, this factor, although it cannot be investigated directly, probably plays at the most only a small part in the reduction in the number of standard trips. The increase in average duration of a standard trip from eight to ten minutes would not, however, entirely account for the drop in the number of standard trips during the sample period.

Graph Fig. 38 shows the average time spent within the nest during the two hour sample period, plotted against the age of the wasp. It will be noticed that the period spent within the nest increases with age after the 14th day.

The fall in the number of standard trips per sample period is thus due both to a reduction in foraging efficiency of the wasp, which takes longer to collect a load, and also to an increase in the length of time spent within the nest between foraging trips.

The time spent within the nest after each foraging trip shows no correlation with the type of substance collected. This is surprising, since the activities within the nest after collection of different types of load are necessarily different. A wasp applies the whole of a load of pulp without the assistance of other workers, but if the load is of fluid or insect flesh other workers help in the distribution of the fluid, and the maxillation and distribution of the insect flesh.

c) STAGE III, Stage of slow increase

The rapid growth of the nest attained during stage II is not maintained. The population increases more slowly and becomes stable at the

end of the stage. The ratio of foraging rate (trips per hour)/ number of workers is lower than in stage II, and the worker/larva ratio higher. The workers do not now commence foraging until 7 - 9 days after emergence (Fig.40). This increase in the time spent in the nest before commencing foraging causes an increase in the average length of life of the workers. Histogram Fig.39 shows the distribution of life spans of the workers. The fact that workers forage less frequently (compare Figs.40 and 36) than in stage II also tends to prolong life. Each worker makes 4 - 5 trips per two hour period during its period of maximum activity, days 8 - 24, as compared with 7 - 8 trips and days 4 - 13 in stage II. From Figs. 41 and 37, it is seen that the average duration of a foraging trip in stage II is similar to that in stage III, showing the same increase with increasing age of the worker. In stage III therefore, the workers spend more time within the nest (Fig. 42). In fact, wasps more than 30 days old rarely leave the nest, but spend most of their time on guard in the nest entrance.

d) STAGE IV, The climax of the colony

The beginning of stage IV is marked by the most important change that takes place within the colony. The workers begin to build queen cells. Once queen cells have been initiated no further worker cells are built. Workers do, however, complete any worker cells in which there is growing brood. Since no more worker cells are built, the worker population cannot increase further, and as males are now being reared in some of the worker cells the population of workers begins to

decrease.

Fig.44 shows that, in stage IV, workers forage more frequently than in stage III; the foraging rate becoming comparable with that in stage II as stage IV progresses (Fig.36). In stage IV they also start foraging sooner after emergence than in stage III. Towards the end of the period they commence foraging after 2 - 4 days. Fig.45, when compared with Figs. 37 and 41, shows that the average duration of a foraging trip in stage IV is similar to that in stages II and III, and increases similarly with age. In stage IV, therefore, the time spent by workers within the nest is less than in stage III (Fig.46). The average length of life of a worker is consequently shortened (Histogram Fig.43).

The workers feed the majority of the food brought into the nest to the queen larvae which, being in the lower combs of the nest, are those which the workers reach first on returning to the nest. This behaviour results in the prolongation of the larval period of the workers and males. Usually, only one generation of queens is reared in each comb, but some of the first formed queen cells may occasionally be used a second time. However, these larvae rarely reach maturity. The season is usually too far advanced by the time the first queen cells are initiated to allow two whole generations of queen brood to be reared before the onset of cold weather and the consequent death of the workers.

e) STAGE V, The decline of the colony

The nest has fulfilled its function. A crop of virgin queens has

been produced, and these will leave the nest, mate, hibernate, and reproduce their kind in the following spring. The queen is now aged and unable to perform her function as mother of the colony, and when she dies the co-ordination of the colony begins to break down. The workers begin to lay eggs. During this stage, cells often contain more than one egg, a characteristic sign of worker oviposition. The foraging rate drops off rapidly when the queen dies, thus causing a reduction in the amount of food being brought into the nest and starvation level is soon reached. The workers then turn cannibal and eat some of the larvae, tearing others from their cells and carrying them out of the nest. Once this has happened, the nest temperature soon falls and the remaining workers either starve or die of cold.

The heat produced in the nest is largely dependent upon the size of the colony. The amount of heat produced is proportional to the volume of the living material (workers and larvae) and the loss of heat is proportional to the surface area of the nest. A wasp nest is approximately spherical and will be considered for the moment as a sphere. As the radius of a sphere increases the surface area/volume ratio decreases. It therefore follows that larger nests are better able to conserve heat than smaller nests, and therefore the workers in the latter build up extra thick envelopes in order to maintain the optimum internal temperature (32° C).

Several workers - Huxley (1937), Krombein (1956), Sailer (1958) and

V NEST TEMPERATURE

When collecting wasp nests it was noticed that the thickness of the paper envelope varied considerably. Aerial nests and nests very close to the surface of the ground always had thicker envelopes than those which were deep in the ground. It was also noticed that smaller nests had thicker envelopes than larger nests.

It was found that workers forage for pulp in response to the nest temperature, as will be shown in a subsequent section. Therefore a consideration of the factors affecting nest temperature will help to explain the above observations. Nests near or on the surface of the ground are obviously less well insulated than those buried deep in the ground, and so lose heat more rapidly. Therefore this is one reason why aerial nests have thicker envelopes than subterranean nests.

The heat produced in the nest is largely dependent upon the size of the colony. The amount of heat produced is proportional to the volume of the living material (workers and larvae) and the loss of heat proportional to the surface area of the nest. A wasp nest is approximately spherical and will be considered for the moment as a sphere. As the radius of a sphere increases the surface area/volume ratio decreases. It therefore follows that larger nests are better able to conserve heat than smaller nests, and therefore the workers in the latter build up extra thick envelopes in order to maintain the optimum internal temperature (32°C).

Several workers - Himmer (1937), Weyrauch (1936), Sailer (1950) and

Gaul (1950) - have made observations on the nest temperatures of species of Vespula. All these observers agree that the nest temperature is regulated to some extent, usually being kept above the temperature of the air at an optimum of approximately 32°C . These authors, however, considered only nests that were situated above ground level.

Underground nests of Vespula vulgaris L. show the same pattern of temperature fluctuation as described by the above authors, only the magnitude of these fluctuations is reduced. The nest temperature is lowest shortly before foraging commences, and then rises slowly to around the optimum during the morning. The nest is maintained at around the optimum temperature until foraging ceases, when the temperature starts to decrease again. If, during the day, the temperature rises above the optimum, the workers fan with their wings and so cool the nest.

correspond to an aerial nest as found in nature. Since, however, the experimental nest was kept constantly at a temperature of 32°C , it cannot be assumed that these observations will reflect exactly the situation found in nature, where the nest temperature fluctuations would affect the relative humidity.

VI NEST HUMIDITY

The humidity of a nest was measured by using a wet and dry junction thermocouple. A large number of fine copper and Constantan junctions were piled alternately and adjusted so as to give no deflection on a galvanometer. The pile was inserted into the nest, one end of the junctions being kept wet by means of wool dipping into a water bath outside the nest. The fluctuations in the nest humidity were then read off the galvanometer.

The humidity in the nest was fairly constant, varying between 85% and 95% Relative Humidity. There was a slight diurnal change, the humidity being highest at night (2-5 a.m.) and lowest at about noon.

These observations were made on a nest kept constantly at 32°C. in a nest box in the laboratory. As regards position, this nest would correspond to an aerial nest as found in nature. Since, however, the experimental nest was kept constantly at a temperature of 32°C., it cannot be assumed that these observations will reflect exactly the situation found in nature, where the nest temperature fluctuations would affect the Relative Humidity.

Observations were made during September and October 1962 on nests of *Vespula vulgaris* L. During this time there was a prolonged period of clear weather with light easterly winds. These conditions gave mean temperatures approaching 10°C. on several occasions, and even lower temperatures on some occasions.

On all occasions when the temperature was below 5°C, there was a

VII FORAGING

A. 1) Flight thresholds of light and temperature

The foraging of the social wasps Vespula sp. is dependent upon light and temperature, and as long as these are above threshold level the wasps will be actively foraging. Taylor (1963) has shown that the flight of Vespula germanica Fab. queens in spring is related to temperature. Gaul (1952), working on the American species Vespula maculifrons Buy., found that the threshold for light was 0.5 foot candles at 9°C. (or above). At lower temperatures the light intensity needed for flight was much greater - 10 foot candles at 8.5°C. Blackith (1958) made a similar investigation of the British species Vespula vulgaris L., Vespula germanica Fab., Vespula rufa L., and Vespa crabro L. From his observations he concluded that light intensity was the significant factor, and that this was independent of temperature. However, it will be shown below that the temperatures at which Blackith was working were too high for any change of threshold to be observed, as his tables show no temperature below 6.1°C., although, in his conclusions, he discusses temperatures of 2°C.

Observations were made during September and October 1962 on nests of Vespula vulgaris L. During this time there was a prolonged period of clear weather with light easterly winds. These conditions gave dawn temperatures approaching 0°C. on several occasions, and even lower temperatures on some occasions.

On all occasions when the temperature was below 5°C. there was a

notable reluctance to leave the nest and forage, although the nest temperature was normal (27°C . or above). The observations showed that Vespula vulgaris L. will not forage at temperatures below 2°C . no matter what the light intensity. On September 28th, a morning on which there was frost at dawn, foraging was not commenced until 8.50 a.m. when the temperature had risen to 2°C . This represented a delay of about two hours after the normal threshold for light intensity had been reached.

If the light intensity at which the first foraging activity commenced is plotted against the temperature $^{\circ}\text{C}$., a graph of similar configuration to that plotted by Gaul (1952) is obtained. The flight threshold of Vespula vulgaris L. is, however, very much lower than that for Vespula maculifrons Buy. The data used when the graph (Fig.47) showing the relationship between the light and temperature thresholds was drawn up were collected when foraging commenced at dawn on many days. Threshold conditions were noted when the rate of two flights per minute from the nest was maintained for three minutes, or increased. This was necessary because, on some occasions, wasps would leave the nest before threshold levels were reached and return after a very short flight, or after having crawled around the entrance.

For the most part of the wasps' active season, (June to October) the temperature is well above the threshold of 2°C ., and so the factor which usually limits the daily period of foraging activity is the light intensity. When the temperature is above 2°C . the wasps begin to leave the nest as soon as the light intensity reaches threshold level. There

is, however, a range of thresholds within any colony due to individual differences between the workers. Certain workers always leave the nest at a lower light intensity than others.

Barlow (1952) discussed the possibility that, in Apis, these individual variations were related to eye length. His theories have been confirmed by Blackith (1958) who showed that the different light intensities at which the British species of Vespula commenced foraging was related to their eye length.

2) Typical daily activity

Fig.48 is a graph of the typical daily foraging activity of a nest of Vespula vulgaris L. (stage III) during a day of fine weather. After the initial awakening of the colony the number of foraging trips increased very rapidly to a high level. After a period at this level, the rate of foraging decreased to a constant level, (normal daily foraging activity). This normal daily foraging activity was then maintained throughout the day until the light began to fade in the evening, whereupon the number of wasps leaving, and therefore returning to, the nest began to decrease until threshold light intensity was reached. Sorties from the nest then ceased. Shortly before threshold conditions were reached there was a period of apparent increased activity. This was due to a large number of workers, which were foraging when the light intensity fell to near the threshold level, returning to the nest while there was still enough light for flight.

The high early morning activity peak is found in all records of

daily activity of species of Vespula. (Gaul (1952) and Blackith (1958)). This early morning activity peak may be explained by any of the following reasons, or a combination of them:-

- i) Larval requirements. After a night without food, larval demand will be high. This may cause increased foraging activity until this demand is satisfied.
- ii) A rapid foraging for fluid (water from the morning dew and nectar which is in rich supply).
- iii) The necessity for the release of excretory products - trophallactic secretions etc. - which have been accumulated by the wasps during the night.

An increased larval demand after a night of starvation may well stimulate all the workers of the appropriate age to forage, and they may maintain their activity until this initial demand has been satisfied. Once this demand has been satisfied, the foraging rate would drop to and remain at the level necessary to maintain a constant supply of food to the larvae. It has been demonstrated that wasp nests in stage III are capable of a greater output of foraging activity than they usually maintain. This will be discussed in the following section.

The total foraging activity shown in Graph Fig.48 is analysed in Graph Fig.49 to show the relative proportions of the three types of foraging activity (pulp, fluid and insect flesh collection) throughout the day, each expressed as a percentage of the whole. From Fig.49 it is seen that, during the early morning peak of activity, the proportion

of fluid collected, relative to other types of foraging, was higher than at any other time of day.

During the early morning when the relative humidity is high and there is dew on the ground, fluid collection is probably easier and therefore more rapidly carried out. There is an abundance of nectar in the flowers due to the morning nectar rise and the fact that no nectar has been collected during the night. These factors would tend to decrease the time needed to collect a load of fluid. The number of loads carried by an individual worker during this period would thus be greater than during a period of similar length later in the day. This was, in fact, noted when, during stage III, a recording of the times taken for fluid collection by individual workers was made from dawn until noon. It was found that the time taken by a wasp to collect a load of fluid was markedly shorter during the early morning than at any later time of day. The time taken in the early morning (c. 6 mins.) was about half that taken at noon (12 - 15 mins.). It was also noted that, after rain-fall following a dry period, the length of time taken to collect a load of fluid was reduced to 3 - 4 minutes instead of the usual 12 - 15 minutes under normal conditions. In this case the wasps probably collected only water. In the same way it is possible that water collection may be a regular morning activity.

It is unlikely that the early morning peak of activity was due to flights for the release of products excreted by the larvae, or by nurse wasps that had not commenced foraging. The number of wasps which had not

started to forage was relatively small, and a single short trip by each of these wasps to release excretory products would be unlikely to increase the foraging rate to such a high level for so prolonged a period.

It thus seems likely that the ease of collection of fluid (nectar or water) in the early morning, and the increased demand by the larvae, possibly associated with an increased number of the workers stimulated by the larvae to forage, are responsible for the early morning peak. Short extra trips for the release of excretory products may play a small part but will not make a very great difference to the foraging rate, as some trips of this nature will continue throughout the day.

3) Effects of bad weather

The foraging of workers is influenced to a certain extent by weather conditions. It has been shown (Gaul 1950) that wasps are unable to foretell the coming of heavy rain. The author confirmed this and also observed that wasps foraged with vigour in heavy rain; only when rain became torrential was foraging interrupted. When a severe rainstorm broke in the area of the nest there was a rapid return to the nest. Again, after the rain had stopped, there was an increase in the rate of returning workers for a short period. (Fig.50). When foraging had been interrupted by a storm the wasps were very reluctant to forage again, even though the weather was calm and dry. (Fig.50). When this type of situation arose, nearly all the foraging after the storm was for fluid. (Fig.51). On days of high wind the same type of behaviour

occurred; there was a reluctance to forage, and most of the activity was the collection of fluid. The workers stood in rows in the nest entrance and remained constantly on guard.

4) The relationship between nest temperature and pulp collecting activity

It has been suggested by Brian and Brian (1948) that the differing number of envelopes built by two queens of Vespula sylvestris Scop. were related to the different light intensities at the nest sites. However, the writer observed that the thickness of the nest envelope made by the wasps was dependent upon the temperature and temperature fluctuations of the nest. Nests in exposed situations have thick envelopes, while those in well insulated positions have thin ones. A nest was artificially warmed by a paraffin heater and cooled by leaving the doors of the nest chamber open. The percentage of the total trips which were for pulp was noted at the different temperatures. Observations were always made between 2 and 3 p.m. so as to minimise the error due to the diurnal change in pulp collecting activity. The results are plotted in Graph Fig.52. Pulp collecting was high when the temperature in the nest was below the optimum, 32°C . However, if the nest temperature dropped as low as 25°C . the rate of pulp collecting fell off considerably.

Experiments were carried out, using the temperature controlled nest box, to determine the percentage number of trips for pulp, insect and fluid collection throughout the day, at temperatures of 32°C ., 28°C ., 26°C ., (Figs. 53, 54 and 55). A small number of trips for pulp (less

than 10% of the total) were made at the optimum nest temperature, 32°C. A drop of 4°C. to 28°C. caused an increase in the number of trips for pulp to between 30% and 40%, and a decrease in the number of trips for fluid and insect flesh. When the temperature was dropped further, to 26°C., the number of trips for pulp decreased to between 20% and 30%. The number of trips for fluid increased, but the number for insect flesh was further reduced.

If a wasp nest, with its envelope removed, is kept at the optimum temperature of 32°C. it might be expected that the wasps would not make any paper envelope. If the nest is kept in the dark, they make very little paper and cover the nest very slowly. When light is not excluded the wasps cover the nest quickly with a very thin layer of paper. Therefore, the rate of paper construction is related to the light intensity, but the thickness of the envelope is related to the nest temperature.

5) The relationship between nest humidity and foraging activity

An experiment was performed to investigate the effect of a lowering of the nest humidity on the foraging behaviour of the wasps. Phosphorus pentoxide was placed on trays over the perforated zinc nest chamber roof. It was, however, found to be difficult to lower the relative humidity of the nest considerably without damaging the nest envelope. The envelope acts as a barrier to air circulation around the nest and thus cuts down the loss of water vapour from the nest. The phosphorus pentoxide was introduced after foraging had ceased in the evening, and

it was found that the relative humidity of the nest had been reduced by about 20 - 25% to 70% R.H. by the time foraging was commenced the next morning. This reduction in the relative humidity resulted in a slight increase in fluid collection and decrease in insect flesh collection (Fig.56). The humidity in the nest rose very slowly throughout the day and by the evening was only about 7% below the evening normal. Foraging activity had also nearly returned to normal, the amount of fluid collected being only slightly increased. In a normal wasp nest the humidity usually falls after the onset of foraging in the morning to about 85% R.H. and remains at this level until the cessation of foraging.

The wasps thus respond to a reduction of Relative Humidity in the early morning, when the Relative Humidity of the nest is normally high, but as the day progresses, when normally the R.H. would be falling, they become less responsive to a lowered R.H.

VII B. Experiments to investigate the factors stimulating foraging

Experiments were carried out to ascertain which was the main stimulus influencing the worker foraging behaviour. The possibilities are that foraging is stimulated by:-

- 1) The brood
- 2) The amount of work to be done
- 3) The queen
- 1) The brood

A nest of Vespula vulgaris L. in stage III was raised a little by

the rod and wheel, and a large piece of comb (c. 900 cells and 700 larvae) was placed under the nest, supported on corks. The nest was then lowered onto the new comb until the inter-comb distance was correct. The nest was then left to settle down. Observations were commenced after 4 days, on the 14th September, 1962.

Graphs Figs. 57 and 58 show the typical daily flight activity of the nest before the experiment (on 9th September) with the typical morning peak, and distribution of foraging activity. On September 14th, observations were made and the graph Fig. 59 obtained. The foraging rate was increased to a level higher than the normal morning peak and was maintained at a higher level throughout the day, although it did decrease slowly until it reached a constant level of about 700 trips per hour at 2 p.m. This level was maintained until foraging was terminated by the decreasing light intensity. Graph Fig. 60 shows the proportions of different substances collected during this activity. Fluid collection was higher than in the normal daily activity although it dropped throughout the day as in the normal daily activity pattern. The amount of insect flesh collected was also higher than normal. Pulp collection was, however, very slight, being only 2% of the whole activity.

Graph Fig. 61 shows the situation 16 days after the implantation of the comb. The foraging pattern was showing signs of returning to normal. The early morning foraging activity was, however, even higher than 4 days after the implantation. This was due to the fact that the worker population had been augmented by hatchings from the implanted

comb. The early morning activity peak was of longer duration than in normal activity, but the foraging rate dropped to a daily normal of 500 trips per hour by noon. The proportion of substances collected during this period of activity (Fig.62) were similar to normal, but more fluid and less pulp were collected in the morning peak period. The amount of pulp collection did, however, remain slightly greater than normal in the evening.

Twenty-four days after the implantation of the comb, activity had nearly returned to normal, graphs Figs 63 and 64. During the morning peak fluid collection was still greater than normal and pulp collection was reduced, but once the daily normal level had been reached the proportions were near to normal.

From this experiment it can be concluded that the nest in stage III is capable of a much greater output of labour than it normally maintains. If there is an increased larval demand the workers will step up their activity to fulfil the demand. The foraging in these circumstances is almost entirely for fluid and insect flesh to feed the larvae, the stimulus from the larvae overriding the stimulus to lengthen the envelope to cover the new comb.

This experiment was repeated in 1963 with similar results. A similar experiment was also performed on a nest in stage II of its life cycle. It was observed that the increase in activity in the stage II nest was not so great as in the stage III nest, showing that there was a much smaller unused labour force in stage II.

B. 2) The amount of work to be done

A nest of Vespula vulgaris L. which was foraging at a constant rate was taken and the envelope was destroyed, thus creating a need for a large amount of constructional work without altering the brood requirements. The result of this was to increase foraging a little, and this increase was entirely in pulp collection for repairing the nest. The rate of repair was slow, complete repair taking 12 days. There was no great increase in labour output as there was in the previous experiment. This result might follow if only young wasps, not older wasps, could make paper. It has been shown that workers become less eager to forage and do so less actively as they age, and there is evidence that they collect more pulp when they first commence foraging than later in their active lives. The implantation of brood might stimulate the older workers to forage more actively (as seen in the previous exp.) but destruction of the envelope would not affect them if, for some physiological reason, such as a reduction of the salivary secretion they were unable to make paper.

If workers and queen are placed in a box with a nest from which all the larvae have been removed, only a very occasional foraging trip is observed until after the 5th day, when larvae have hatched from the newly laid eggs. This also indicates that the stimulus to forage given by the larvae is more powerful than that given by a need for constructional activity, as repair to the envelope did not commence until foraging for fluid to feed the larvae had started.

B. 3) The influence of the queen

On September 3rd 1962 the queen was removed from the Vespula vulgaris L. nest and placed in a box with some comb, brood and workers. On the previous day the foraging rate in nest No. 2 during the daily normal period was 800 trips per hour. The next day the foraging rate in the queen - less nest was very much depressed and on September 5th it was very low - Fig. 65. The low rate of foraging was associated with an almost complete cessation of pulp and insect collection (Fig. 66). The queen was now replaced in the nest and as she ran inside, several of the workers tried to bite her. Once inside the nest, they accepted her and paid little attention to her. The next day the foraging activity had returned to normal.

This experiment clearly shows the importance of the queen in relation to the foraging activities of the workers.

B. 4) Conclusion and discussion

It is apparent that wasps forage in response to stimuli from within the nest and not as a result of an inherent drive. If the larval demand increases, the wasps forage harder until the demand is fulfilled. If constructional work is created by damaging the nest, there is a small increase in the rate of pulp collection, but the increase is limited, probably by the number of wasps capable of paper making. From graph Fig. 60 it can be seen that the stimulus to collect food - fluid and insect flesh - overrides the stimulus to repair the nest.

The queen, however, is the most important factor influencing the

foraging of the colony, for without some stimulus from her the workers do not respond to other stimuli to forage.

As the worker foraging rate is related to the larval demand (Fig. 59), it is of interest to ascertain how the larvae stimulate the workers to forage. Wheeler (1923) observed that the larvae sometimes turned their heads backwards until the mouth parts made contact with the paper of their cells, and then scratched the paper with their mandibles. This, he suggested, attracted the attention of the nurse workers and thus secured food for the larvae.

Preliminary observations were made by the writer, and it was noted that the frequency of cell scraping by the larvae increased with the time between their feeds. The larvae of Vespa crabro L., however, did not behave in the manner described by Wheeler. These larvae rotated their bodies and stretched their heads backwards. They then contracted their bodies rapidly, bringing their heads forwards and scraping their mandibles down the side of the cell ventral to their bodies.

the nest, and they run out into the entrance tube. This may be a response to the sound produced by the wasps giving the defence reaction.

When looking at a wasp nest in stage III or IV, it is seen that there are, at all times of day, a small number of workers apparently on guard in the entrance. These wasps are only numerous when the nest is of a fairly large size. They are, however, present during stage II at certain periods (morning, evening and during bad weather). When considering the activity of workers in stages II, III, and IV, it was

VIII DEFENCE

As has been previously described by Gaul (1953), it was noticed that, if a wasp nest is disturbed, it is only the wasps leaving the nest that give defence flights or attack an intruder. Wasps returning to the nest take no notice of the disturbance and try to enter the nest. (It should be noted that these observations were made on a nest with a simple, undivided entrance tube). If a wasp nest is repeatedly jerked, the workers soon cease to give defence flights, and become tolerant of the disturbance. When a wasp nest is first given a jolt, the guards take up a characteristic attitude. They rise onto the tips of their tarsi, and, with heads forward, and abdomens turned down, are in an arched position, their wings constantly vibrating. This position is similar to that taken up by wasps when fanning to control the nest temperature. However, when giving the defence reaction, the wing beat appears to be shorter and the frequency is probably higher. This reaction seems to elicit a definite response from the workers within the nest, and they run out into the entrance tube. This may be a response to the sound produced by the wasps giving the defence reaction.

When looking at a wasp nest in stage III or IV, it is seen that there are, at all times of day, a small number of workers apparently on guard in the entrance. These wasps are only numerous when the nest is of a fairly large size. They are, however, present during stage II at certain periods (morning, evening and during bad weather). When considering the activity of workers in stages II, III, and IV, it was

seen that workers forage less, and spend longer within the nest, as they age. It is these ageing workers which act as the guards of the nest. Wasps more than 30 days old can often be seen standing in the entrance tube examining returning foragers for hours on end. All foraging wasps within the nest will, however, come to the defence of the colony if the need arises.

The typical daily activity of wasps apparently guarding the nest in the entrance tube is shown in Fig. 67. There is a gathering of wasps in the entrance tube shortly before foraging commences, but, once the threshold light intensity is reached, the foragers leave the nest, and only the guards remain throughout the day. Later in the day when the light is fading, the number of wasps in the nest entrance increases until foraging ceases, when some of them return to the nest for the night.

When the weather is stormy, and unfavourable for foraging, the number of guards in the entrance is very much increased (Fig. 68). This increased number is due to the reluctance of the workers to forage. Under these conditions, the nest is very easily upset, and the defence reaction and flight easily elicited.

IX DIVISION OF LABOUR

In the previous sections it has been seen that the foraging behaviour of the workers is regulated to a large extent by the physical conditions within the nest, and the larval demand for food. It has also been seen that a wasp's activity and the length of a wasp's life are related to the stage of the colony development. These factors complicate the discussion of a temporal division of labour.

When the initial stages of the nest were discussed, it was seen that the queen exhibited a distinct pattern of foraging behaviour, and, since in the initial stages of the nest she performs all the duties later performed by the workers, it is of interest to examine this pattern. After founding the nest, the queen collects only pulp for nest construction until the first larva hatches in the nest. She then commences to collect fluid and then, later, insect flesh. As insect flesh collection increases, the collection of pulp decreases, and finally stops. The collection of insect flesh, however, is only of limited duration and slackens off and finally ceases at about the time that the first workers emerge. Fig. 69 shows the distribution in time of the different foraging activities of the queen.

Division of labour during stage III will next be considered, for, at this stage, the life span of a wasp is at its longest and the changes in behaviour are more protracted and therefore more easily followed. For the first few hours after hatching the young workers take no part in the life of the colony. They often remain motionless, with their heads

inside a cell, for quite long periods. During stage III workers do not generally forage until about seven days after hatching. The first week of the workers' life is spent acting as a nurse, feeding the larvae, helping to maxillate the insect flesh and distribute the fluid brought in by the foragers, removing trophallactic secretions from the larvae, and destroying and remaking the paper envelopes. The early foraging trips made by the young workers are for pulp, with a few trips for fluid. After a few days, the proportion of pulp begins to decrease, and the wasps start to collect insect flesh and more fluid, although some pulp is still collected. The collection of pulp has usually ceased by the time the wasps are about 18 days old. Insect flesh is collected mainly between days 14 and 22, and fluid is collected all the time. Workers over about 24 days of age collect only fluid. After 30 days, the wasps spend proportionately more and more time in the nest entrance acting as guard wasps, and only make an occasional foraging trip. These occasional sorties may be of very long duration, often lasting up to an hour or more. Fig. 70 shows diagrammatically the distribution in time of the various activities of the workers and Fig. 71 shows the foraging activities of a group of 30 wasps in relation to their age.

The data used when drawing up this graph (Fig. 71) were collected during a daily two hour period - 10 - 12 a.m. and 3 - 5 p.m. on alternate days. The numbers of trips for pulp, fluid, and insect flesh collection made by the sample of 30 workers of the same age were noted. In order that any diurnal fluctuations in foraging activity should be minimised,

the results from each two consecutive observation periods were summed. Therefore a set of figures was obtained which represented the number of trips for pulp, for fluid, and for insect flesh made during four hours, (10 - 12 a.m. and 3 - 5 p.m.), in a two day period. These figures were collected throughout the life of the workers. Expressed as a percentage of the total number of trips taken, these figures were plotted against time to obtain the Fig. 71.

The pattern of foraging behaviour of the queen is closely followed by the workers. The workers, however, commence to forage for pulp and fluid as soon as they begin foraging, whereas the queen collects only pulp initially. The innate foraging patterns in the workers and the queen are probably identical, the above difference being caused by the fact that the workers have brood to feed in the nest, whereas the queen lacks this stimulus.

The small number of queens found in the nest during this investigation can probably be explained by the fact that the old queen had become infertile, possibly by the exhaustion of her sperm supply. Rottner (1956) showed this to be the case in the honeybee. This situation would result in only a few queens being reared, and these in the first queen cells which had been built. The queen, however, appeared to be perfectly healthy when the nest was taken, the workers were foraging actively, and superfluous eggs had not been laid by the workers.

X POLYMORPHISM

a) The dimorphism of male *Vespa crabro* L.

In September, 1961, a large nest of *Vespa crabro*, which was producing sexuals, was taken at Chudleigh, Devon. The wing length of all the adults was measured and the results plotted in histogram form.

The wing length of the females, (workers and queens), showed the expected bimodal distribution (Fig. 72), showing that the castes were morphologically separate (Blackith, 1958). The histogram for male wing length (Fig. 73) was also bimodal. Many of the capped cells contained teneral adults which had not emerged. These were removed by cutting off the cell caps. It was thus possible to show that males from queen cells were considerably larger than those from worker cells. The males are therefore affected by the cell size in the same way as the females. The photograph Fig. 74 shows a male from a queen cell and two males from worker cells.

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A similar dimorphism is also found in Vespula vulgaris, but, since very few males are reared in the queen cells of a normal, healthy colony, the incidence of large males is small.

b) Caste determination

Caste in the various groups of the Vespidae is probably determined in several different ways. Only in the Vespinae are queens clearly differentiated from the workers, and reared in different sized cells. In other families of the Vespidae the castes are not clearly differentiated, and are reared in uniformly sized cells. Richards and Richards (1951) suggested that a decrease in the larva/worker ratio might result in the rearing of sexuals, if sexuals developed from larvae that had had extra attention from the workers. They showed that, on theoretical grounds, the larva/worker ratio would decrease as the colony grows, if the life span of a worker is longer than the generation time and if one worker feeds more than one larva. The writer has shown that this situation exists in Vespula vulgaris nests. More attention would, therefore, be given to the larvae as the colony grows. This might be the only mechanism of caste determination necessary in those groups in which the sexuals and workers are reared in the same sized cells.

The discovery that male Vespa crabro show dimorphism, which is correlated to cell size as in the female, suggests that the important factor in caste determination in the Vespinae might be the cell size. This, linked with an ample food supply, might be the only factor necessary for queen differentiation. Queen cells are usually built at the bottom

of the nest and are thus nearest the entrance, so the larvae obtain food from the returning foragers. It is possible that the size to which larvae grow in their last two instars might be governed by a thigmotactic relationship with the cell wall. An examination of the larval instars from queen and worker cells revealed that the larvae of the first three instars from each type of cell were of similar size and it appeared that the difference in growth occurs in the last two stages (Fig. 75).

Richards and Richards (1951) discussed caste determination in the Vespidae. The writer has examined those of their theories which could apply to the Vespinae. As caste in the Vespinae is influenced by cell size, the important question is what factors influence the change in behaviour from worker cell construction to queen cell construction. These factors are considered in the following discussion of Richards and Richards' theories:-

a) Trophallaxis

A variation in the trophallactic balance might affect the castes. Possibly a change in larva/worker ratio would cause a change in trophallactic balance and this might trigger queen cell initiation.

b) Cyclical factors

i) It is apparent that the photoperiod has nothing to do with initiation of queen cells since some large nests produce queen cells early in the year, whereas some small nests never produce queen cells. If queen cell production were related to photoperiod, all nests of the same species would produce queens at much the same time of year.

(ii) The larva/worker ratio is one of the simplest types of cycle exhibited by the nest, and this might play some part in the initiation of queen cells.

(iii) Deleurance (1946 and 1948) has shown that the life cycle of Polistes is dependent on the age of the queen. If nests of Polistes gallicus were kept at a constant temperature and with a constant supply of food, the colonies produced sexuals after a set interval of time, regardless of the comb size or population.

The writer carried out three experiments which throw more light on the subject of queen cell initiation. The first experiment was designed to see if the larva/worker ratio had any influence on queen cell initiation. Two nests of Vespula vulgaris L., each with about 500 workers, were taken, and all the workers of one nest were introduced into the other colony. This effectively decreased by half the larva/worker ratio in the second nest. The result of the experiment was that the foraging rate was slightly increased, and the morning peak was higher and of very short duration. Most of the additional foraging was for pulp for building more comb which consisted of worker cells. After three weeks the behaviour was unchanged and no queen cells had been initiated. It is thus apparent that the larva/worker ratio does not influence queen cell initiation in the Vespinae.

On August 6th 1962, a large nest of Vespula vulgaris L., in which some queen cells had recently been built, was set up in an observation box. The queen was removed and replaced by a queen from a small nest,

which had initiated no queen cells, and the existing queen cells were destroyed. No more queen cells were built, the nest grew rapidly, and the cell construction was all of worker cells. Queen cells were not initiated in this nest until September 28th 1962.

The reverse experiment was also performed. The old queen was introduced into the small nest and queen cells were initiated within a week of the introduction of the physiologically old queen.

These experiments show that the initiation and building of queen cells is related to the physiological age of the queen. The queen stimulates the workers to build either small worker cells or large queen cells.

Two other theories, discussed by Richards and Richards (1951), which may affect the differential development of the larvae within worker and queen cells, are considered below:-

a) Differential feeding

At present, no instance of this is known. Pardi (1942 and 1946) failed to notice any different type of feeding in Polistes, and the author has noticed only a difference in frequency of feeding, not in quality, in Vespula.

b) Theory of oösrption

This theory was put forward by Flanders (1942, 1945 and 1946). It proposed that workers developed from eggs laid at a low rate, during maximum oösrption, and that queens developed from eggs laid at a high rate, during minimum oösrption. It is a fact that the rate of

oviposition usually increases throughout the season. This theory, however, is not supported by Deleurance (1946 - 1948) who was able to induce Polistes gallicus L. to produce queens before any workers had hatched.

c) The dominance of the queen

One of the most important problems of colonial life in the Vespinae is that of social co-ordination. In some way, the co-ordination of a healthy colony is maintained so that only the queen lays eggs. As has been seen when discussing foraging, if the queen is removed the foraging rate drops and the workers begin to lay eggs.

The maintenance of the dominance of the queen and the social co-ordination of the nest might be effected by two means - a pheromone or a psychological factor. Pardi (1946) showed that in Polistes gallicus, when several females aggregate and found a colony in the spring, one female develops a psychological dominance over the others by aggressive behaviour towards them. This results in the slow degeneration of the ovaries of the other females, while the ovaries of the dominant female develop and she becomes the only egg layer. In nests of Vespula vulgaris which may contain many thousands of cells, up to ten comb levels, and often have more than 3,000 workers, it is difficult to imagine how the queen could terrorise all the workers and prevent their ovipositing in some of the cells at the different comb levels. The writer has never seen the queen make an aggressive approach to a worker as has been described by Pardi (1946). A chemical factor would thus seem a more

likely means by which the Vespula vulgaris queen maintains dominance in the colony.

On one occasion, when taking a nest using trichlorethylene as an anaesthetic, the queen was very badly affected and it was feared that she would die. However, she eventually recovered and was seen ovipositing two days later. On the 8th day, some cells contained more than one egg, a sign that the workers were ovipositing. After this the queen lived for another ten days, during which time she was seen to oviposit. The heavy anaesthetising of the queen had thus in some way interfered with her dominance over the workers.

This is further evidence that, in Vespula vulgaris, the queen maintains her dominance by means of a chemical factor. It has been observed that worker wasps pay no attention to the queen, as do worker bees. Numerous writers have observed that bees frequently lick the queen, while worker wasps only occasionally approach the queen to feed her. It is likely, therefore, that the chemical factor by which the queen wasp maintains her dominance is an air-borne pheromone.

From these two colonies no seasonal differences.

The material collected in 1962 can be used to clarify this situation to some extent. Table IV summarises the material collected. Three types of nest were found in the fourth nest, D. These are:

- 1) A hard, thick-walled, hexagonal section (Fig. 79) containing a larva (Fig. 78) in the autumn. These larvae pupate in the spring and produce adults of V. vulgaris.

XI PARASITES

During 1962, four nests were collected which contained cocoons of the Ichneumonid wasp parasites belonging to the genus Sphecophaga. Until 1937, only one species, S. vesparum Curt. was recognised in Britain. In 1937, however, Perkins found two other species mixed in collections under the name of S. vesparum (Curt). (1828). These two species he recognised as S. sericea Thompson (1888) and S. thuringiaca Schmiedeknecht (1914). When Curtis's material was re-examined, it was found to correspond to S. sericea, so S. vesparum is equivalent to S. sericea. Schmieder (1939) has thrown some doubt on the validity of distinguishing between the species S. vesparum and S. thuringiaca. His evidence is based on the American species, S. burra, which has been equated with S. vesparum by Townes (1962). Schmieder believed that the two different types of cocoon, said to distinguish the species were, in fact, produced by the same species. The thick-walled cocoons were the over-wintering cocoons, and the thin-walled ones those of the summer generation. He explained the slight difference in the adults hatching from these two cocoons as seasonal dimorphism.

The material collected in 1962 can be used to clarify this situation to some extent. Table IV summarises the material collected. Three types of cocoon were found in the fourth nest, D. These are:-

- i) A hard, thick-walled, hexagonal cocoon, (Fig.77), containing a larva (Fig.76) in the autumn. These larvae pupate in the spring and produce adults of S. vesparum.

- (ii) A soft, thin-walled, hexagonal cocoon, (Fig.78), containing, in the summer, either the pupa or larva of S. thuringiaca.
- (iii) A soft, thin-walled, wedge-shaped cocoon (Fig.79). These cocoons contained adults which were indistinguishable from S. vesparum, except for their much smaller size.

TABLE IV

	DATE	SPECIES	NEST SIZE (No. of workers)	PARASITES
A)	3/7/62	<u>V. vulgaris</u>	3	6 <u>S. vesparum</u>
B)	4/7/62	<u>V. germanica</u>	17	1 <u>S. vesparum</u> (emerged August)
B2)	7/7/63	<u>V. vulgaris</u>	1,200	hatched <u>S. thuringiaca</u> cocoons
C)	7/10/62	<u>V. vulgaris</u>	3,000	2 empty <u>S. vesparum</u> cocoons 1 <u>S. vesparum</u> 2 adult <u>S. thuringiaca</u>
D)	9/10/62	<u>V. vulgaris</u>	1,500	39 cocoons <u>S. vesparum</u> 5 empty " " " 7 cocoons <u>S. thuringiaca</u> 23 empty " " " 15 cocoons) of a 18 empty cocoons) different species to those described

From these observations it can be concluded that both the species S. vesparum and S. thuringiaca are at least double-brooded. Empty cocoons of both species were found in July and August. Later in October, overwintering cocoons of S. vesparum, and cocoons containing S. thuringiaca adults were found in nest D. It would seem, therefore, that S. vesparum and S. thuringiaca are separate species, and not different forms of the same species hatched at different times of the year, as suggested by Schmieder for S. burra.

The adults emerging from the wedge-shaped cocoons (Fig.79) cannot, as yet, be separated from S. vesparum. It is unlikely, however, that they are simply a smaller form of S. vesparum, because their cocoons were found together with empty and full cocoons of S. vesparum, in the same comb level of nest D. The wedge-shaped cocoon may be either a polymorph of S. vesparum, possibly caused by the eggs being laid on a very young wasp larva, and the resulting larval parasite being starved, or it may be the cocoon of a different, though morphologically very similar, species.

During the later part of July, August and September, all nests of Vespula vulgaris were found to contain the parasitic beetle, Metoecus paradoxus. The presence of the parasite is only apparent in capped cells, as the Metoecus larva does not leave its host and feed externally until the cocoon has been spun. Cells containing Metoecus larvae (Fig.80) contrast with those containing wasp larvae in that they have an ivory-white appearance. This is caused by the thoracic segments of the Metoecus

larva being pressed to the cell cap as it feeds, curled over the head of the wasp larva.

The degree of parasitisation of V. vulgaris nests by M. paradoxus was noted. It was never found that more than 3% of the capped cells were parasitised. The degree of parasitisation was highest in early August, and parasitisation was rare after the middle of September. This explains why Blackith (1958) found it so rarely, as he examined nests in late September and October.

The low incidence of both Sphecophaga and Metoecus indicates that neither of these parasites have much effect on the population growth in wasp colonies.

Blackith (1958) observed this pattern of behaviour in Vespa maculifrons Say. Blackith (1958), however, failed to notice it in any of the British species of wasps because he did not make any observations on really cold mornings.

During the majority of the wasps' year, foraging commences when the light intensity reaches threshold level and builds up rapidly to a high level (the morning peak). After a short period at this high level, the rate declines to a daily normal level. Most of the foraging during this morning peak is for fluid. Gaul (1950) speculated that this early morning peak was either to collect food for the larvae, which had undergone a night of starvation, or for the release of excretory waste products, which had been built up during the night. Fluid is usually more readily available in the early morning than at any other time of day.

XII DISCUSSION

Until this work, no attempt has been made to investigate the foraging behaviour of any species of Vespula, or to discover what factors influence the foraging pattern. The external factor which limits the foraging activity of wasps throughout the majority of the nest history is light intensity. Wasps can usually be seen actively foraging whenever the light intensity is above threshold, that is about one hour before sun rise to one hour after sun set. It is only during the very early stage of nest development in May, and again at the end of the nest history in October, that the temperature is likely to be below 5°C., at which level the temperature modifies the flight threshold. Gaul (1952) observed this pattern of behaviour in Vespula maculifrons Buy. Blackith (1958), however, failed to notice it in any of the British species of wasps because he did not make any observations on really cold mornings.

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and it has been shown by the writer that the length of time needed to collect a load of fluid increases as the morning progresses. It is possible that the early morning peak of foraging is for fluid to satisfy an increased larval demand.

It can be concluded that the gross foraging activities of workers are dependent upon the natural nest cycles, temperature, humidity, and larval demand. This latter is an expression of the foraging activities which are limited by the physical conditions external to the nest. In the morning, when the temperature of the nest is below optimum, the workers collect more pulp, and as the nest temperature rises, the collection of pulp decreases. The temperature of the nest influences the amount of insect flesh collected, because pulp and insect flesh are mainly collected by workers of about the same age, and as the nest temperature rises pulp collection is replaced by insect collection. The foraging for fluids is dependent upon larval demand, and to some extent on the humidity of the nest.

During stage II, the foraging rate in the wasp nest is directly proportional to the number of workers, and, during this stage, this factor actually limits the foraging rate. However, when the worker/larva ratio increases in stage III - probably because the egg laying capacity of the queen is limited - the foraging rate is no longer directly proportional to the number of workers, but to the larval demand. If the larval demand is increased, the foraging rate of the nest increases. The presence of a healthy queen is in some way very important in main-

taining the foraging activity of the nest. If the queen dies, the foraging rate of the nest drops off rapidly.

The writer has shown that a temporal division of labour exists. This, however, is not very sharply defined as wasps of all ages will occasionally forage for all substances within a short period. This division of labour is not very easy to recognise because the time scale of activities is very varied. For example, wasps age rapidly in stage II, when they work longer hours and make more foraging trips per hour, than in stage III, and consequently the division of labour pattern is foreshortened. Workers show the same type of foraging pattern as the queens. A worker first acts as a nurse, then, when foraging commences, collects mainly pulp and a little fluid. As pulp collection begins to decrease, insect collection increases. This then decreases and fluid collection increases. When the workers are at the end of their life span they act as guard wasps for longer periods, and forage much less frequently.

When discussing caste determination, it was shown that male Vespa crabro L. exhibit dimorphism in a manner similar to the females, and that this is related to the size of the cell in which they were reared. There is no difference in the weight of worker and queen larvae in the first three instars in the fixed, outward-facing stage, a difference being detectable only in instars four and five. This indicates that the determining factor between the castes may be the relationship of the larva with the cell wall. This raises the question as to what influences

the construction of queen cells. This has been shown to be related to the age or physiological condition of the queen, but as yet there is no evidence as to how she exerts her influence. An air-borne pheromone is a possible explanation. Vespula vulgaris L. could conveniently be divided into five stages - the solitary stage, the stage of rapid increase, the stage of slow increase, the climax of the colony (queen production), and the decline of the colony.

2) The early development of a nest of Vespula vulgaris was observed from its initiation until it had seven workers. The activities of the queen and the brood sequence were recorded. The normal generation time was found to be about 25 days. The larval stage could be divided into five instars, the first three being fixed facing outwards from the centre of the comb, and the last two being free to move and facing the axis of the comb.

3) The effect of ageing on the activity of the workers was investigated. It was found that the life span of workers was about 17 days in stages II and IV, but increased up to 35 days in stage III. This length of the worker's life was found to be dependent on the larva/worker ratio, and when this ratio is high (stages II and IV), the workers forage more actively, age more rapidly, and die sooner than when the larva/worker ratio is low (stage III).

4) A study of the foraging activity of wasps showed that light was the most important factor determining the length of the wasp's foraging day. Temperatures of below 5°C. could, however, modify this threshold.

XIII SUMMARY

- 1) Many wasp nests were taken in the field, and the adult and brood populations were counted. From these observations it was apparent that the life history of a nest of Vespula vulgaris L. could conveniently be divided into five stages - the solitary stage, the stage of rapid increase, the stage of slow increase, the climax of the colony (queen production), and the decline of the colony.
- 2) The early development of a nest of Vespula vulgaris was observed from its initiation until it had seven workers. The activities of the queen and the brood sequence were recorded. The normal generation time was found to be about 25 days. The larval stage could be divided into five instars, the first three being fixed facing outwards from the centre of the comb, and the last two being free to move and facing the axis of the comb.
- 3) The effect of ageing on the activity of the workers was investigated. It was found that the life span of workers was about 17 days in stages II and IV, but increased up to 38 days in stage III. This length of the worker's life was found to be dependent on the larva/worker ratio, and when this ratio is high, (stages II and IV), the workers forage more actively, age more rapidly, and die sooner than when the larva/worker ratio is low (stage III).
- 4) A study of the foraging activity of wasps showed that light was the most important factor determining the length of the wasp's foraging day. Temperatures of below 5°C. could, however, modify this threshold. A

graph of the typical daily foraging activity shows a high peak in the early morning, later declining to a relatively constant daily normal. The reasons for this early morning peak and its significance are discussed. It was found that the amount of pulp brought into the nest is dependent upon the temperature of the nest. When the temperature is below the optimum, the amount of pulp collected increases.

5) Experiments were carried out to investigate the factors influencing the foraging of the workers. The two most important factors were found to be the presence of the queen and the brood size. It was found that, if the queen was removed from the nest, the foraging rate dropped rapidly to about 10% of the daily normal activity. If the amount of brood was increased in stage III by implanting brood from another nest, the foraging rate was quickly increased.

6) Some light was thrown on the problem of the biology of the Ichneumonid wasp parasites of the genus Sphecophaga. The two species S. vesparum (Curt.) and S. thuringiaca (Schmiedeknecht) ~~were~~ found and their cocoons are described and illustrated. A third type of cocoon, very different from the others, was also found but as yet the adults emerging from it cannot be separated from S. vesparum.

7) It was found that male Vespa crabro L. show a dimorphism exactly comparable with that exhibited by the females of the species. The size of imago is related to the size of the cell in which it was reared. Caste determination and differentiation are discussed in the light of these observations. The onset of queen cell construction was shown to

be related to the physiological state or age of the queen, and not to climatic conditions or nest population. for providing me with laboratory facilities in the Zoology Department of the University of Bristol, and Dr. H.E. Hinton for advice and encouragement during his supervision of this work. I am indebted to the Forestry Commission for allowing me to erect my observation hut on their land. I would also like to thank Dr. D.C.R. Lincoln for help in collecting wasp nests, often late at night.

XIV ACKNOWLEDGEMENTS

I wish to thank Prof. J.E. Harris for providing me with laboratory facilities in the Zoology Department of the University of Bristol, and Dr. H.E. Hinton for advice and encouragement during his supervision of this work. I am indebted to the Forestry Commission for allowing me to erect my observation hut on their land. I would also like to thank Dr. D.C.R. Lincoln for help in collecting wasp nests, often late at night.

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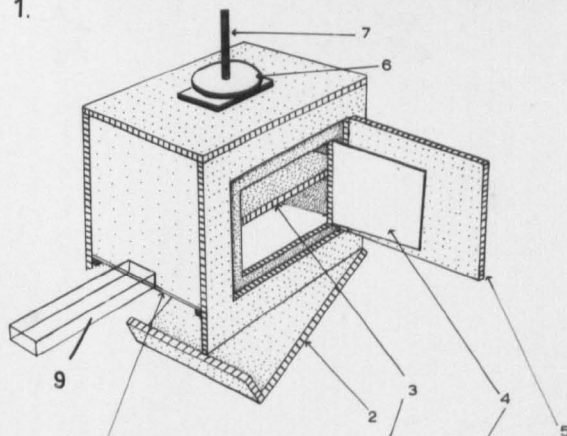
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Fig. 1 Diagram of box used for housing wasps

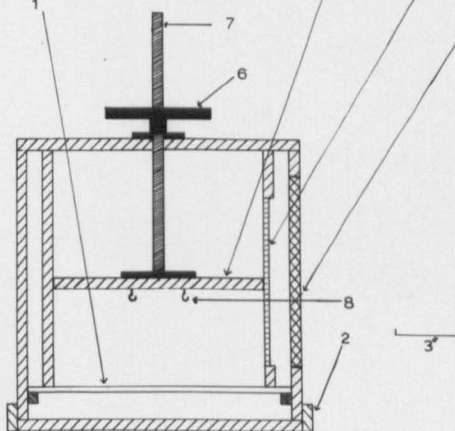
Fig. 2 Section of Fig. 1, drawn to scale

- 1) Glass to allow observations
- 2) Hinged wooden bottom to cover 1) when not in use
- 3) Moveable wooden chamber roof to which nest is attached by hooks (8)
- 4) Perspex door to inner chamber
- 5) Wooden door to outer box
- 6) Wheel for raising chamber roof (3) by means of threaded rod (7)
- 7) Threaded brass rod
- 8) Hooks to allow nest attachment to roof
- 9) Entrance tube

1.



2.



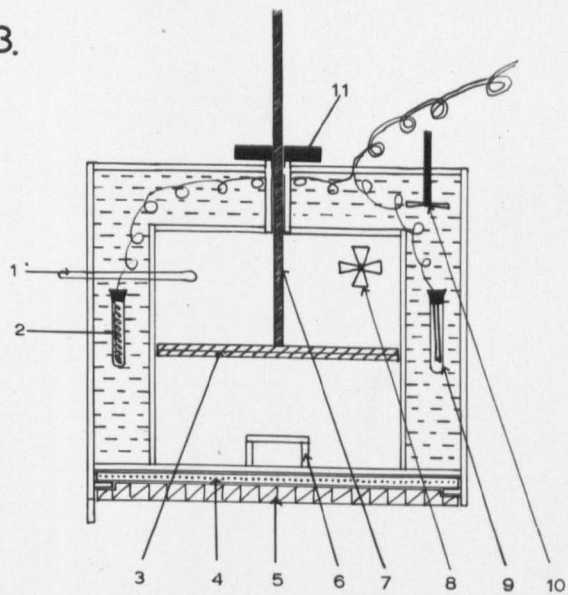
Figs. 3 and 4 Diagrammatic sections through
 temperature controlled box for
 housing wasp nests

Fig. 3 Vertical section

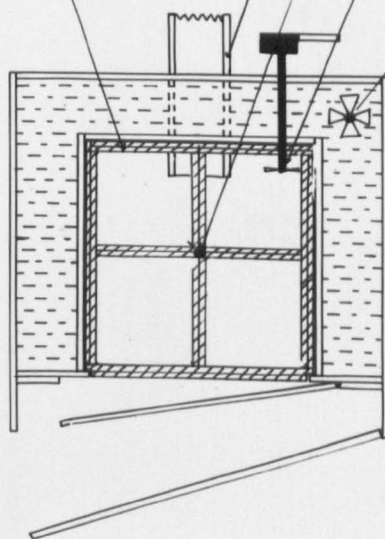
Fig. 4 Horizontal section

- 1) Thermometer
- 2) Heater
- 3) Moveable chamber roof - aluminium struts supporting
 perforated zinc cover
- 4) $\frac{1}{4}$ " plate glass bottom of nest chamber
- 5) Removeable fibre-board insulating layer
- 6) Entrance tube
- 7) Threaded brass rod for raising nest chamber roof
- 8) Fan agitating air in nest
- 9) Thermostat controlling heater
- 10) Fan stirring water in water jacket
- 11) Wheel for raising chamber roof (3) by means of threaded
 brass rod (7)

3.



4.



Figs. 5 and 6 A diagram of the perspex nest
entrance tube incorporating a
double circuit photoelectric
counter for counting entrances
and exits to and from the nest

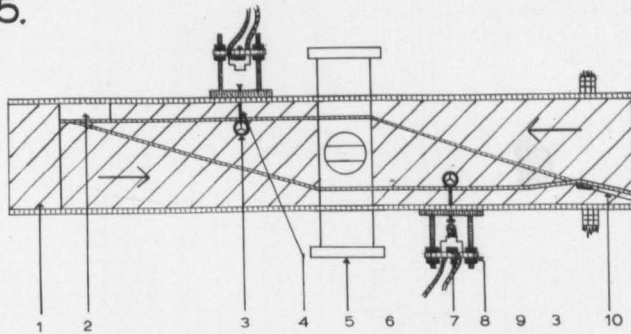
Fig. 5 Plan view of tube

Fig. 6 Side view

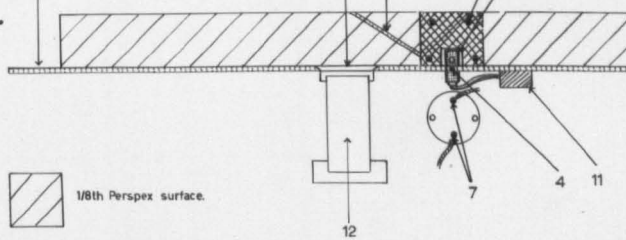
- 1) Alighting board
- 2) Exit hole
- 3) Photo-transistor (Mullard O.C.P.71)
- 4) Transistor locking screw
- 5) Moveable slide to allow wasps to be caught in tube (12)
- 6) Baffle to ensure wasps break light transistor beam
- 7) Bulb holder (to hold pre-focus bulb)
- 8) Bulb mounting bolts
- 9) Adjustable screws to allow alignment of light source
- 10) Spring to prevent wasps leaving by entrance passage
- 11) Cable lock
- 12) Glass specimen tube (1" x 3")

Fig. 7 Circuit diagram of double
channel photoelectric counter

5.



6.



1/8th Perspex surface.



1/8th Perspex edge.



1/16th Perspex edge.

3 ins.

7.

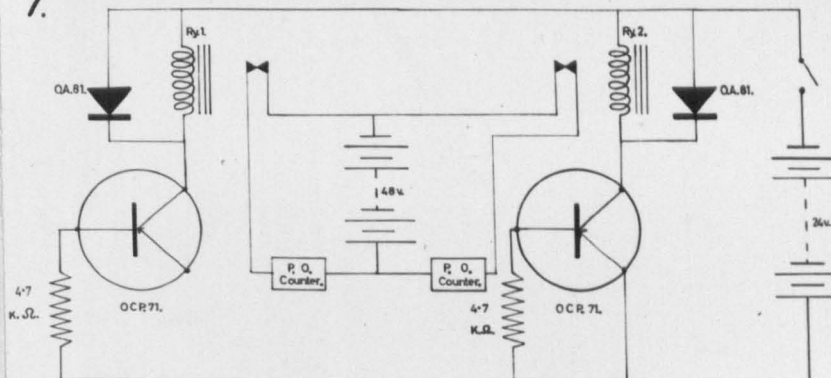


Fig. 8

A diagram showing the population
growth in a successful wasp nest

workers	♀♀
males	♂♂
queens	♀♀

8.

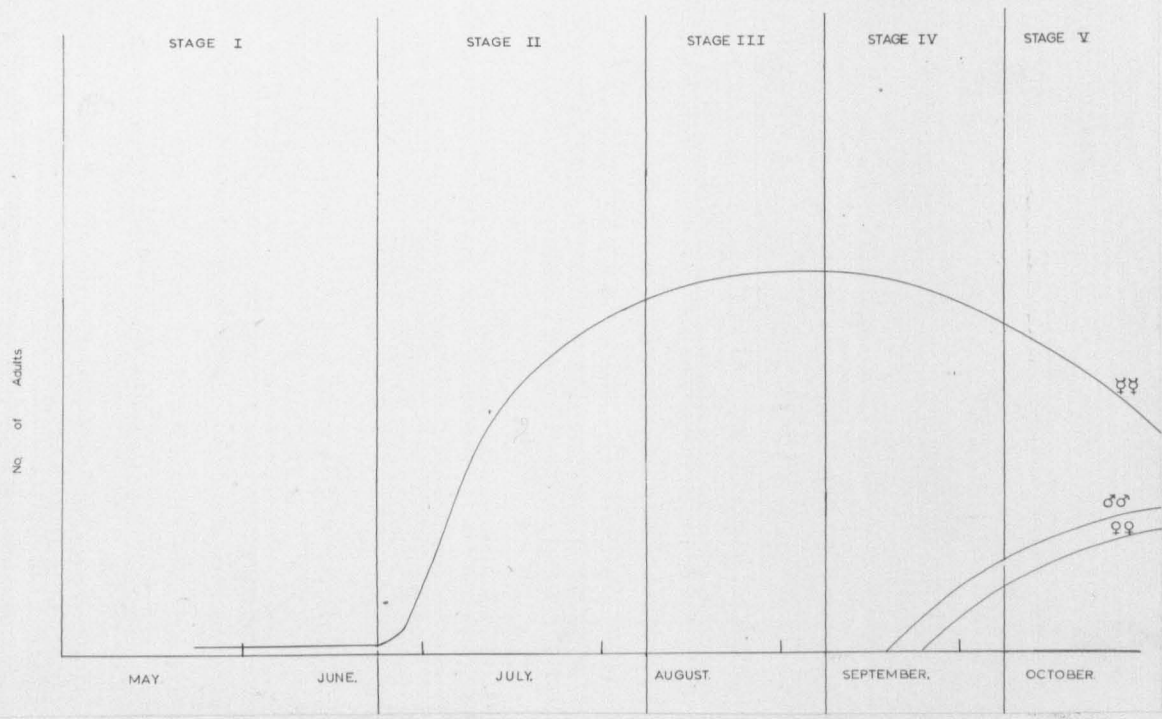


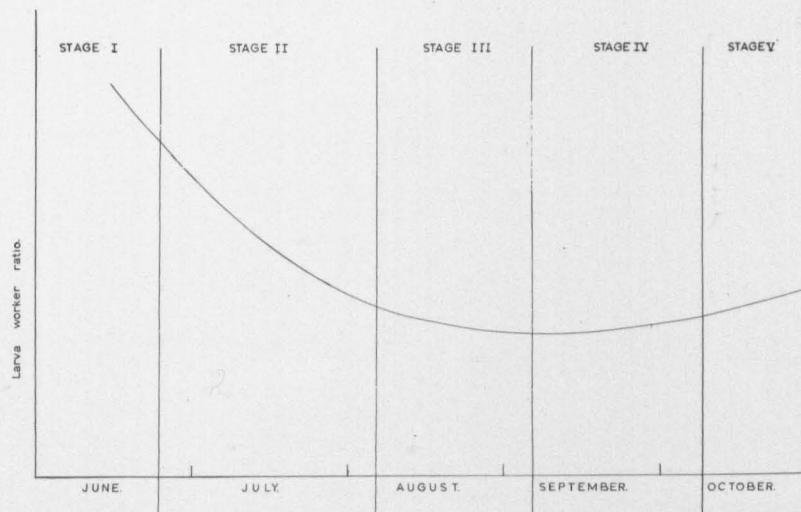
Fig. 9

Diagram showing the changes in larva /
worker ratio during the life history
of a wasp nest

Fig. 10

Diagram showing the rate of cell
construction in a wasp nest

9.



10.

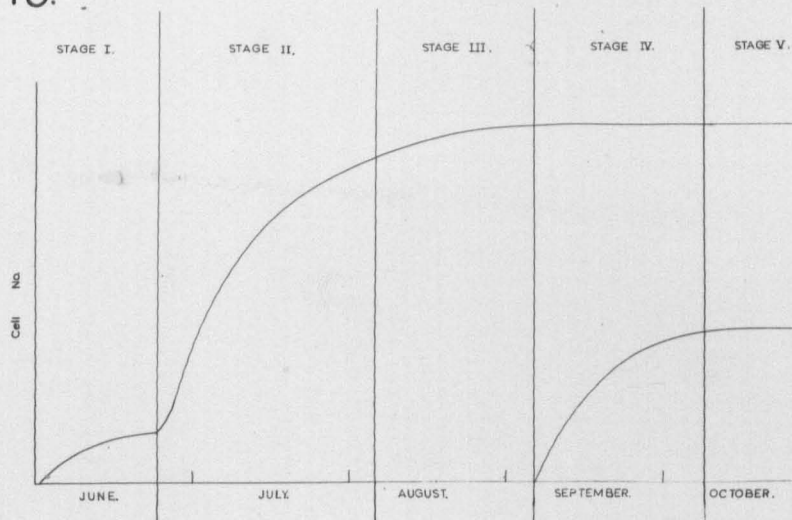


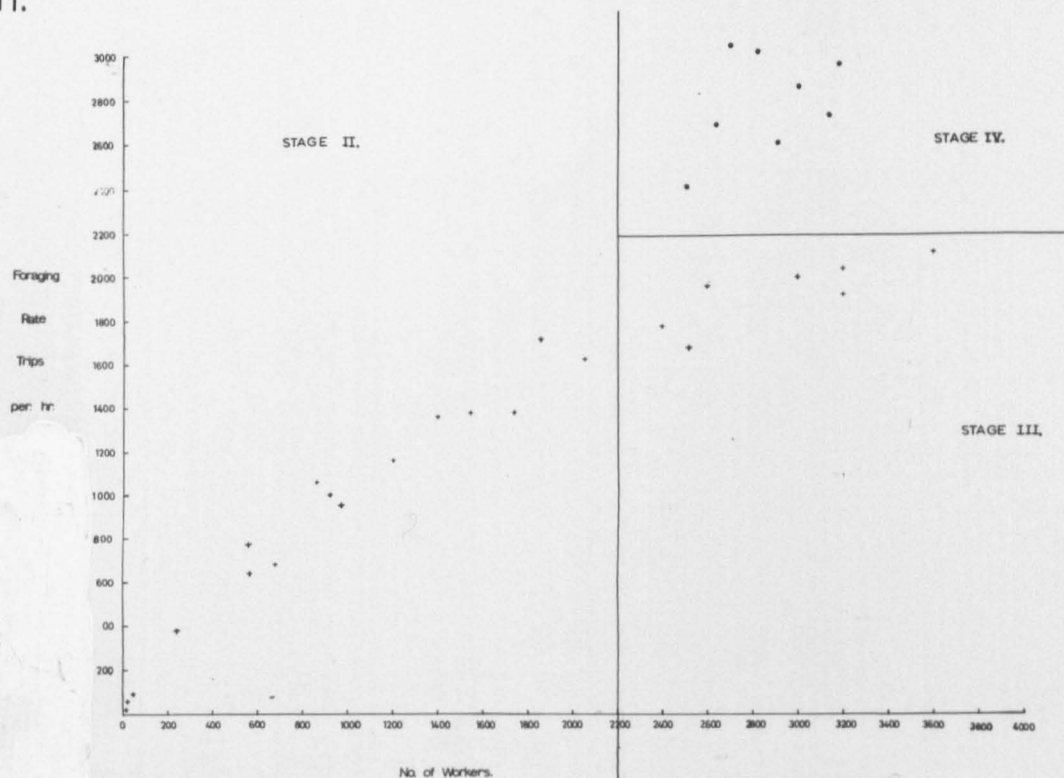
Fig. 11 Foraging rate is plotted against worker population.

- + - Data derived from nests before the construction of queen cells.
- - Data derived from nests in which there were queen cells.

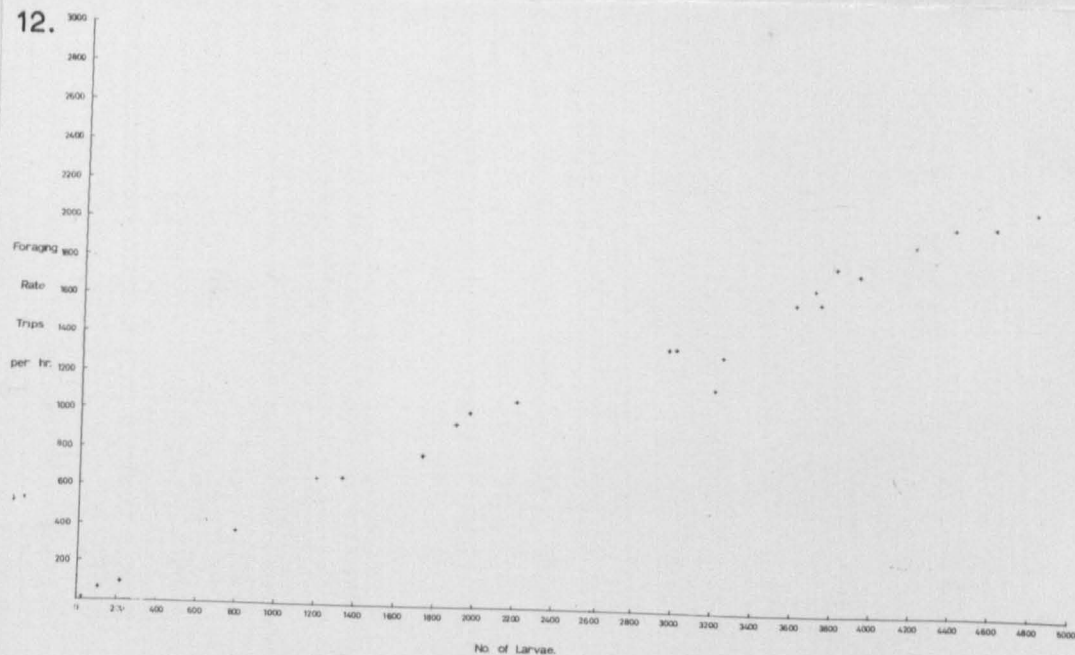
Fig. 12 Foraging rate is plotted against the number of larvae

(See appendix for tabulation of data from which these graphs were drawn)

11.



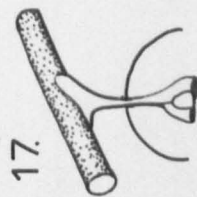
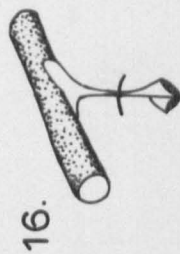
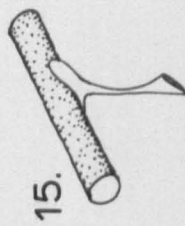
12.



Figs. 13-17

Diagrammatic illustrations of the initial stages of construction of a nest of Vespula vulgaris L. to the end of the second day of construction.

- Fig. 13 Suspension sheet
- Fig. 14 Suspension sheet and beginning of spindle
- Fig. 15 Initiation of first cell
- Fig. 16 Cells two and three started, and also
the first envelope
- Fig. 17 Further development of envelope and cell
construction



Figs. 18-20

Successive stages in nest
construction by a Vespula vulgaris
queen, with cell sequence.

Fig. 18

The first envelope complete

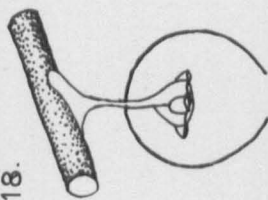
Fig. 19

Envelope two complete

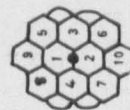
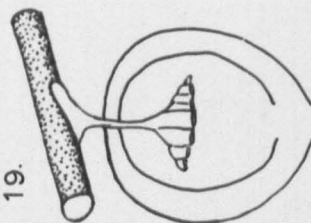
Fig. 20

Envelope three complete, and the first
envelope mostly destroyed

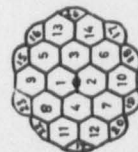
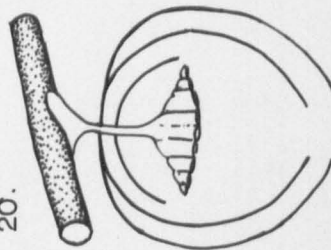
18.



19.



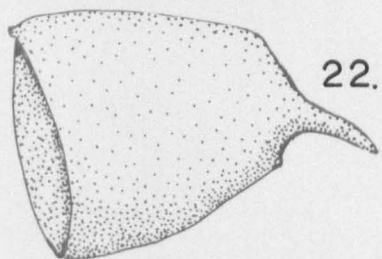
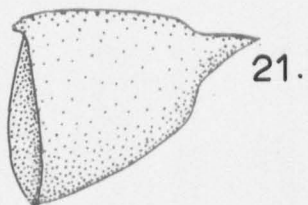
20.



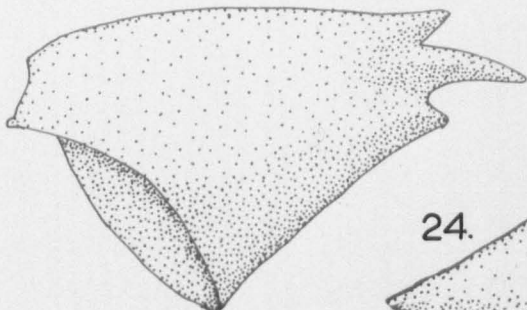
Figs. 21-25

Mandibles of the larval instars
of Vespula vulgaris L.

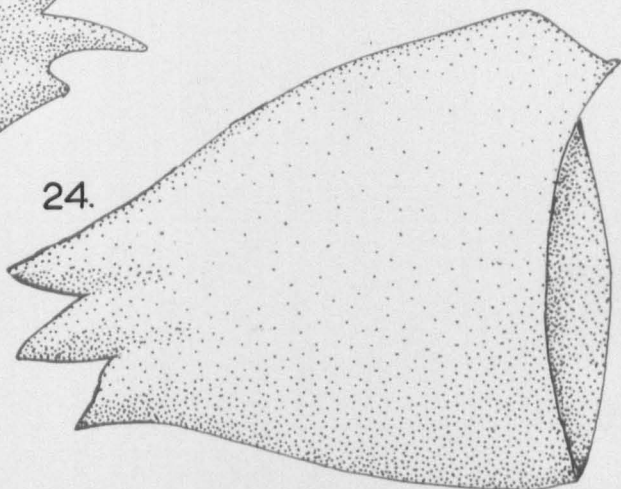
Fig. 21	1st. larval instar)	
)	
Fig. 22	2nd. larval instar)	outward-facing stage
)	
Fig. 23	3rd. larval instar)	
)	
Fig. 24	4th. larval instar)	
)	inward-facing stage
Fig. 25	5th. larval instar)	



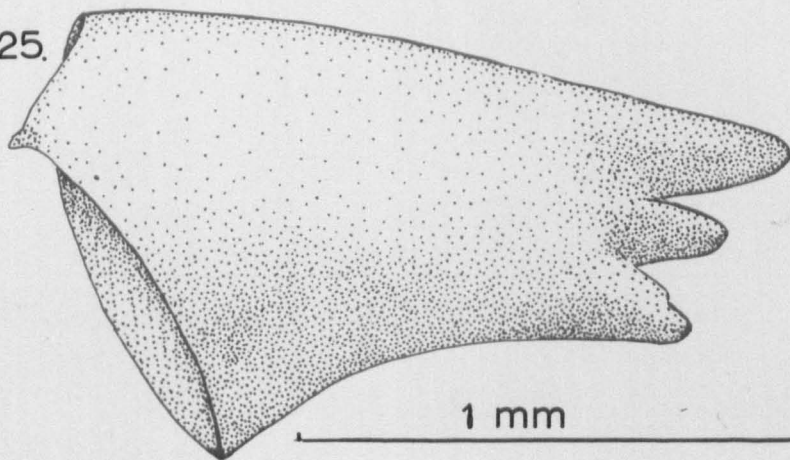
23.



24.



25.



1 mm

Fig. 26

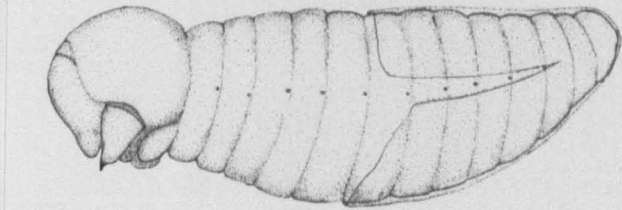
Vespula vulgaris L. First larval instar,
fixed outward-facing stage, within
egg shell

Fig. 27

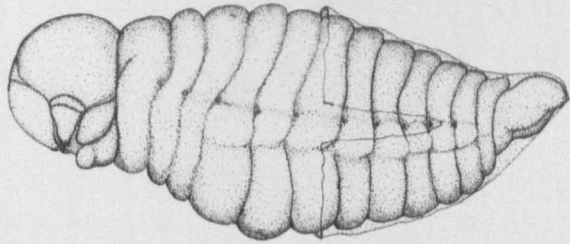
Vespula vulgaris L. Second larval instar,
Fixed outward-facing stage, still with
body within egg shell

Fig. 28

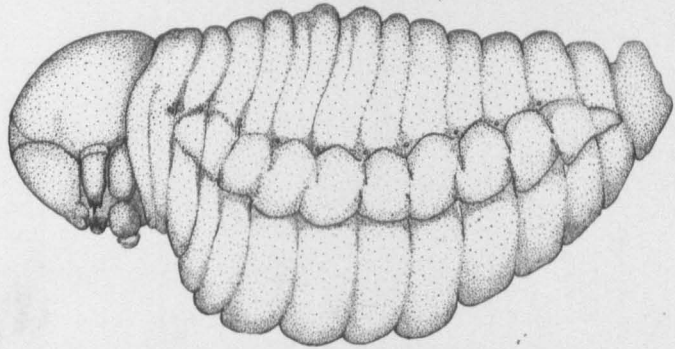
Vespula vulgaris L. Third larval instar,
fixed outward-facing stage



26.



27.



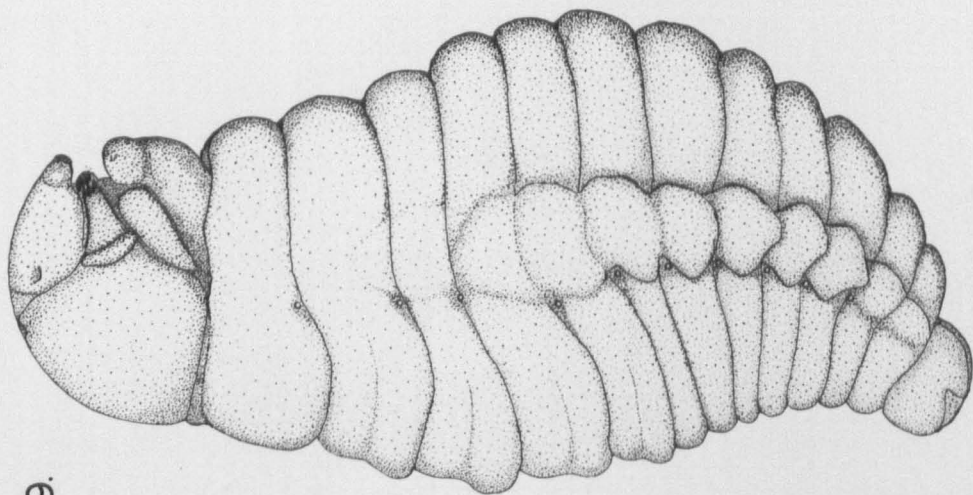
28.

Figs. 29 and 30

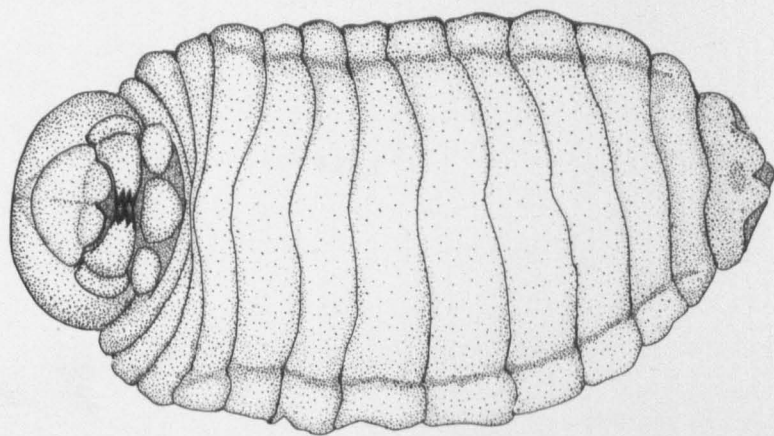
Vespula vulgaris L Fourth larval

instar, the first free-moving,

inward-facing stage



29.



30.

Fig. 31

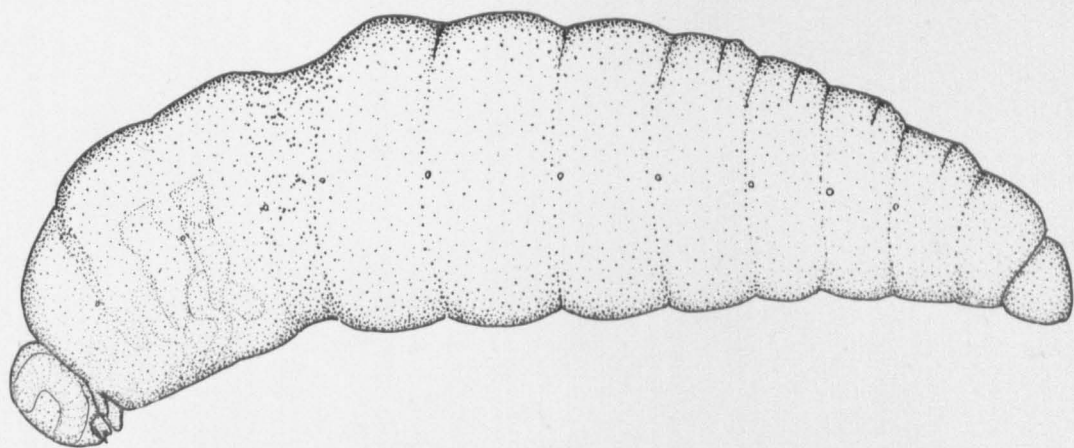
Vespula vulgaris L. Fully grown fifth
instar larva, about to spin a cocoon

Fig. 32

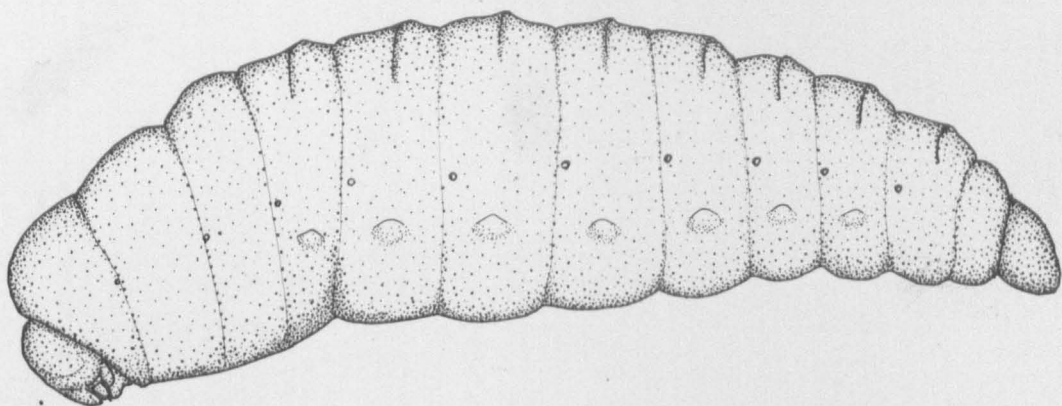
Vespula vulgaris L. Early pharate pupa.
After cocoon spinning, the pupal thorax
is beginning to become demarked

Fig. 33

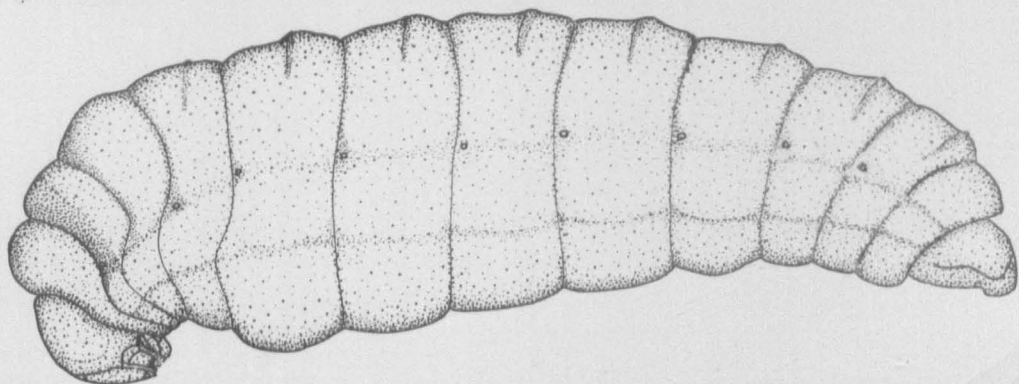
Vespula vulgaris L. Pharate pupa. Thorax
strongly demarked, legs, wings and
antennae visible through larval cuticle



33.



32.



31.

Fig. 34

Chart showing the brood sequence in a
nest of Vespula vulgaris L.

1 - outward facing stage, instars 1-3

L - inward facing stage, instars 4 and 5

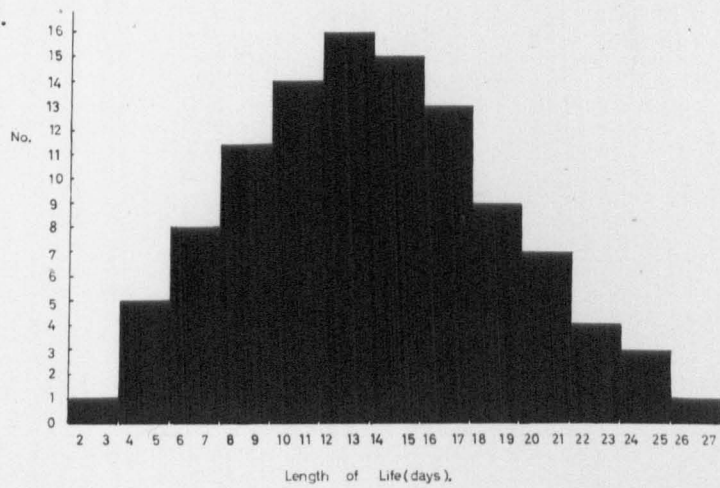
34.

Days.

Fig. 35

Histogram showing the distribution of
life span of workers wasps in a nest
of Vespula vulgaris L. during stage II.

35.



Vespula vulgaris nest, stage II

Fig. 36

Graph showing the number of foraging trips during a two hour period as the wasp aged. The number of standard trips per two hour period is plotted against the age of the wasp in days.

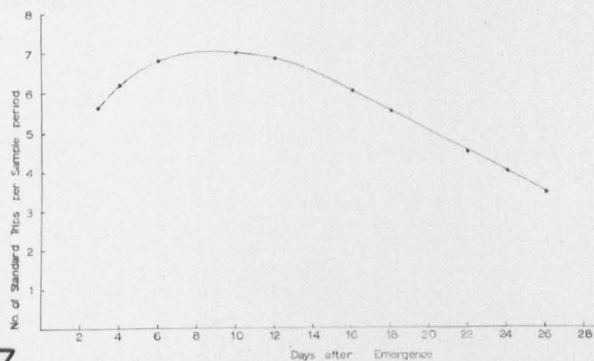
Fig. 37

Graph showing the length of time needed to collect a load at varying ages of the wasp. Average duration of a foraging trip is plotted against the age of the wasp in days.

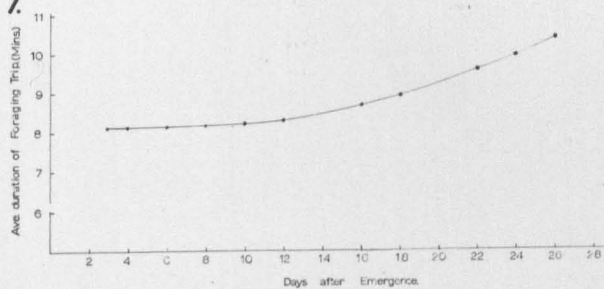
Fig. 38

Graph showing the amount of time spent within the nest during the two-hour period as the wasp ages. Time spent within the nest is plotted against the age of the wasp in days.

36.



37.



38.

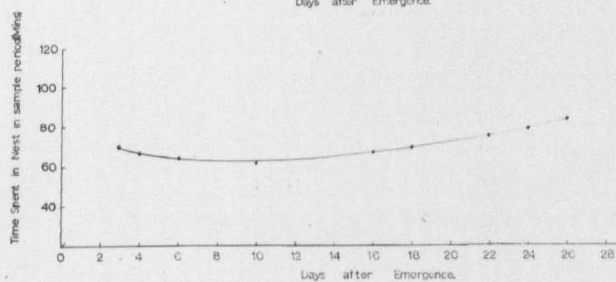
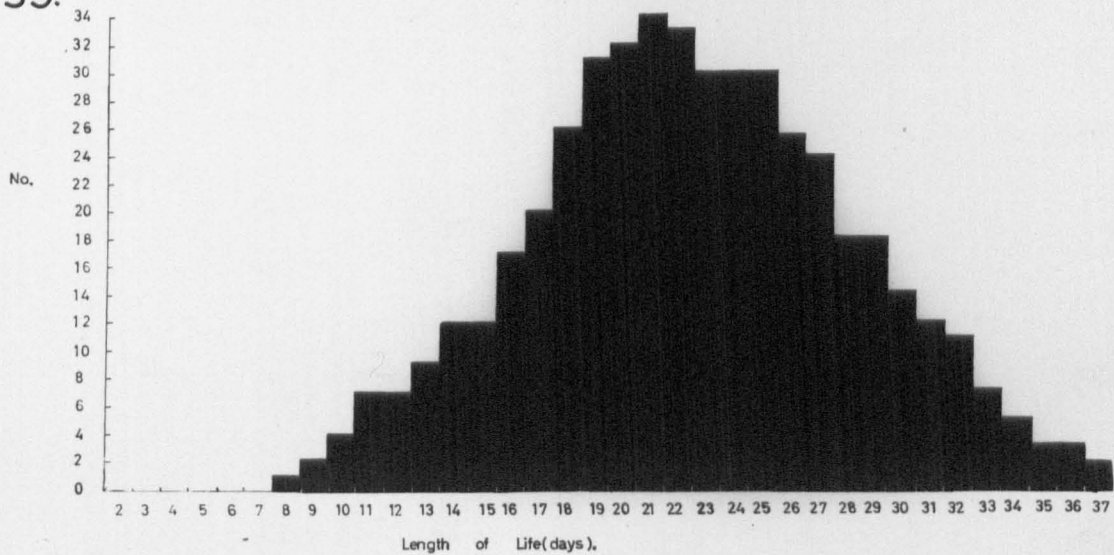


Fig.39

Histogram showing the distribution of life
spans of worker wasps in stage III

39.



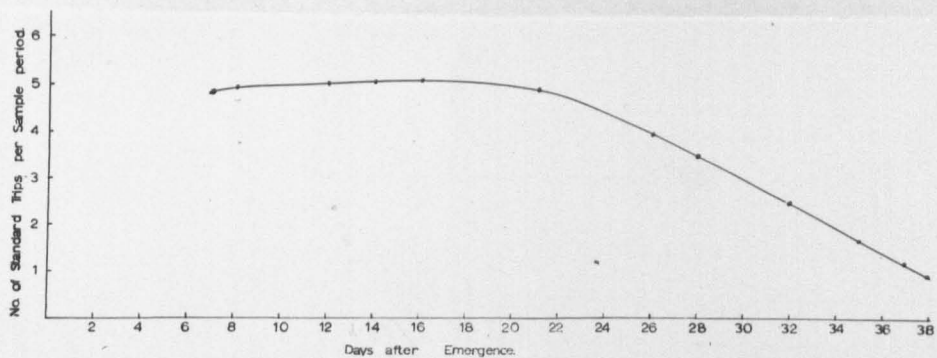
Vespula vulgaris L. nest, stage III

Fig. 40 Graph showing the number of foraging trips
in a two hour period on progressive days
during stage III, plotted against the age of
the wasp in days.

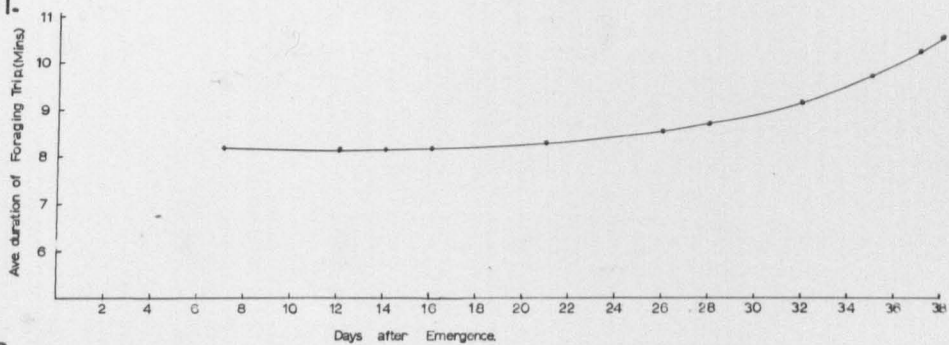
Fig. 41 The average duration of a foraging trip in
stage III, plotted against age.

Fig. 42 Time spent within the nest in a two hour
period, plotted against the age of the
wasp in days.

40.



41.



42.

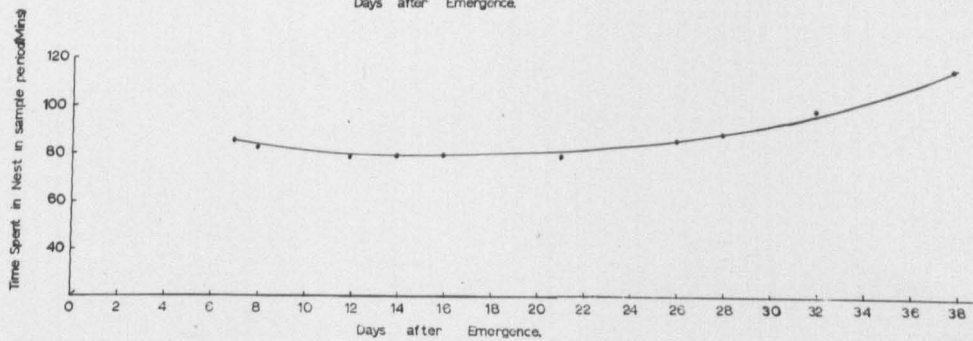
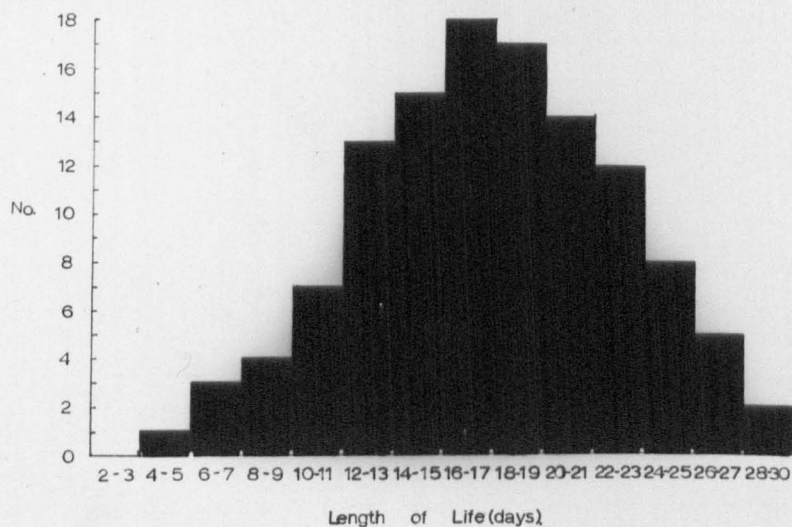


Fig. 43

Vespula vulgaris L. Histogram showing the
distribution of life spans of worker wasps in
stage IV.

43.



Vespula vulgaris L., stage IV

- Fig. 44 Graph of no. of standard trips in a two hour period plotted against the age of the wasp in days.
- Fig. 45 Average duration of a foraging trip plotted against the age of the wasp in days.
- Fig. 46 Time spent within the nest in a two hour period, plotted against the age of the wasp in days.

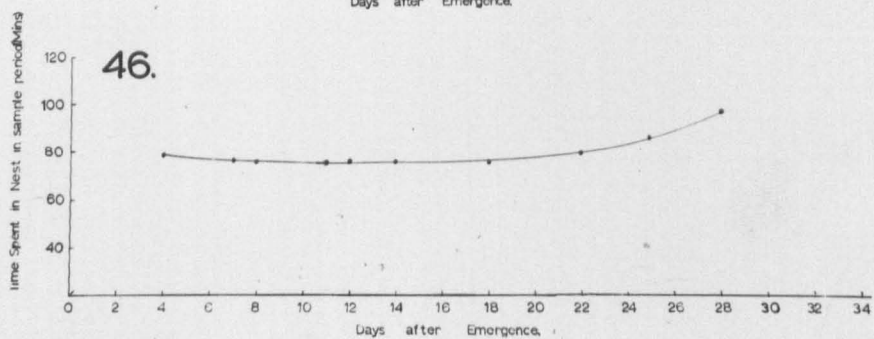
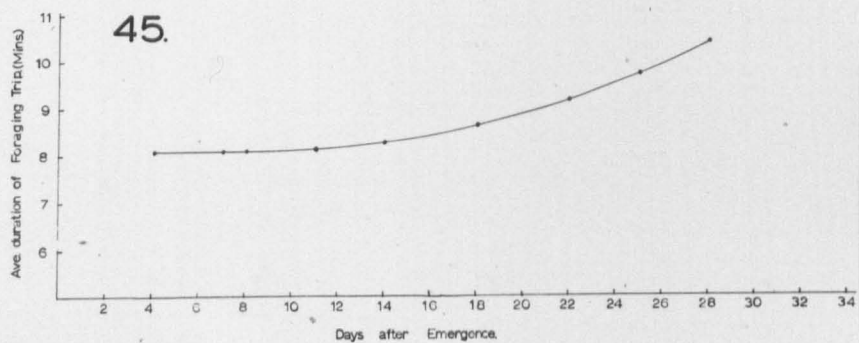
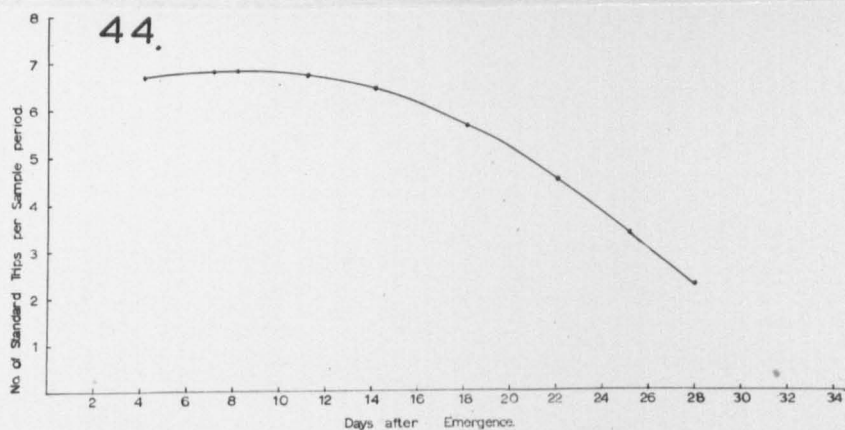


Fig. 47

Graph showing the relationship between
light intensity and the temperature at
which foraging was commenced by Vespula
vulgaris L.

47.

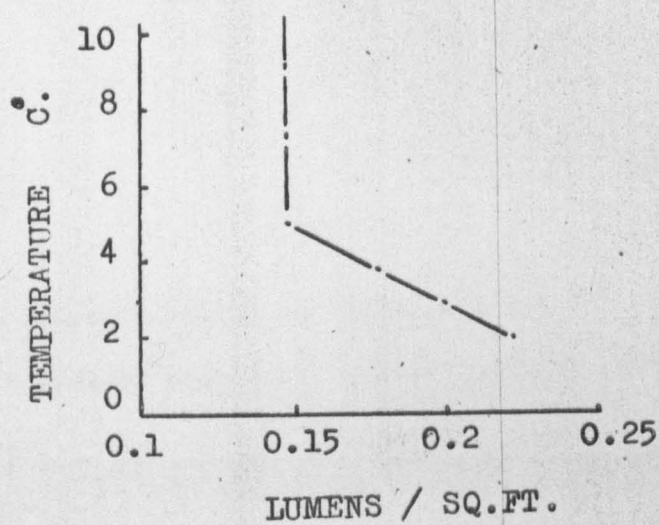
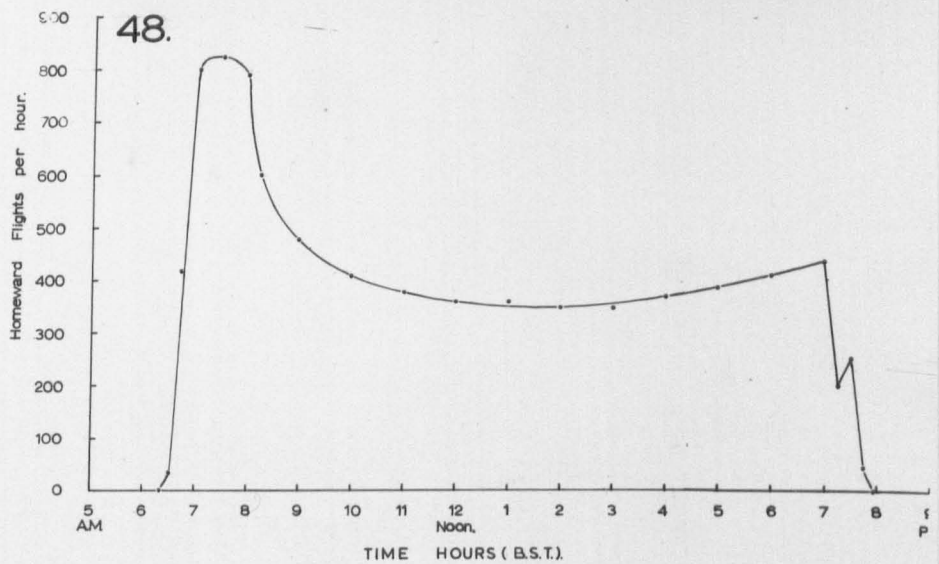


Fig. 48

Graph of typical daily flight activity in a
Vespula vulgaris nest on 7/9/62

Fig. 49

Graph showing the relative proportions of the
three types of substance collected on 7/9/62



49.

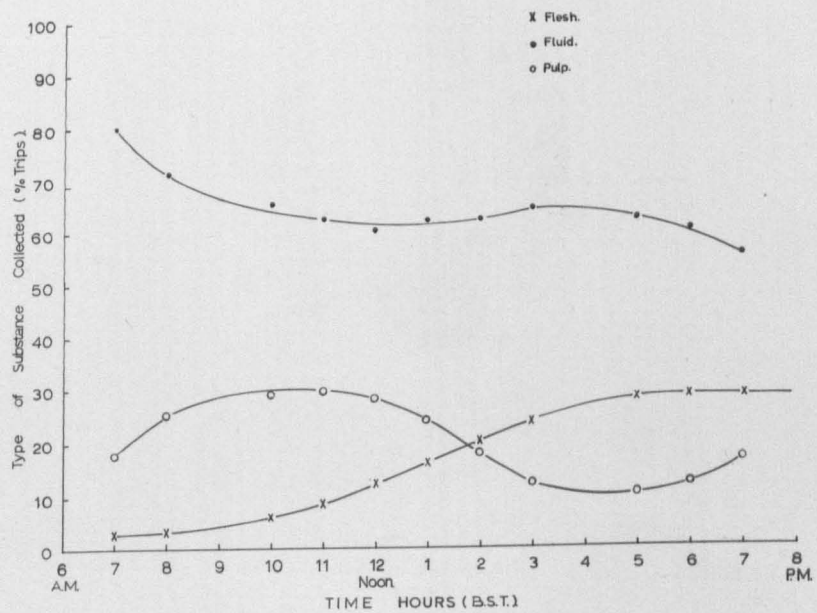


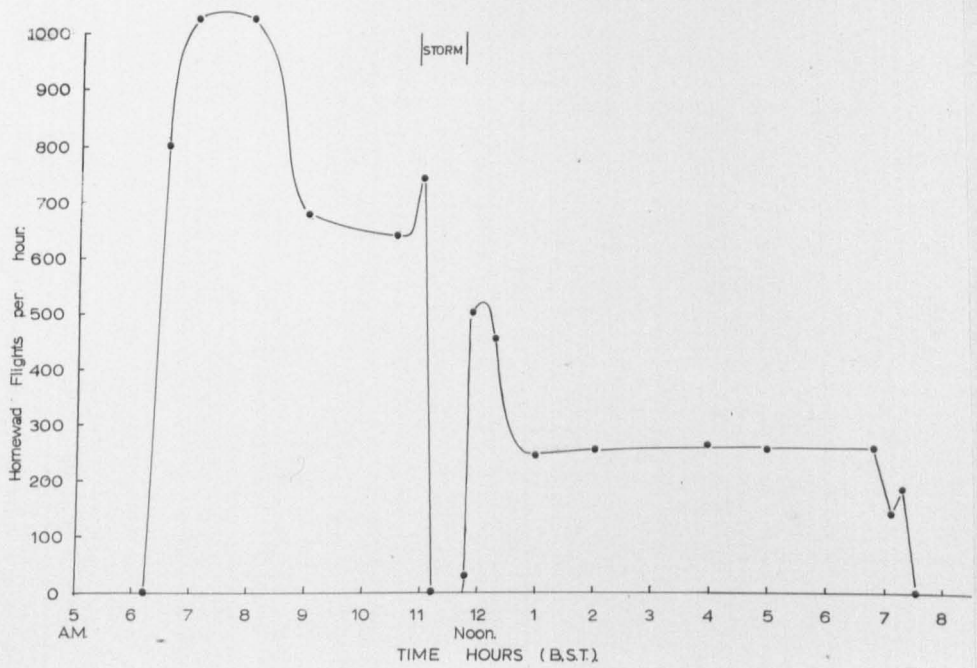
Fig. 50

Graph showing the foraging activity of a Vespula vulgaris nest on 26/8/62, a day on which there was a very severe storm soon after 11 o'clock. This caused a complete cessation of foraging. When foraging recommenced it remained at a very low level for the rest of the day.

Fig. 51

Graph showing the relative proportions of substances collected during the above activities. In the reduced activity after the storm more fluid was collected, and less pulp and insect flesh.

50.



51.

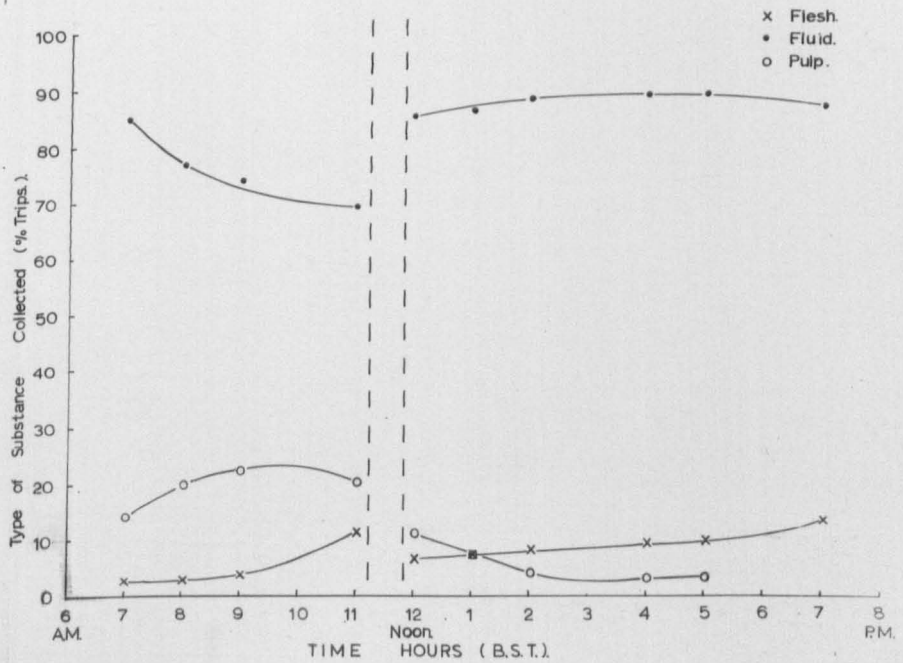


Fig. 52

Graph showing the amount of pulp (% of total trips) collected at different nest temperatures by workers of Vespula vulgaris L.

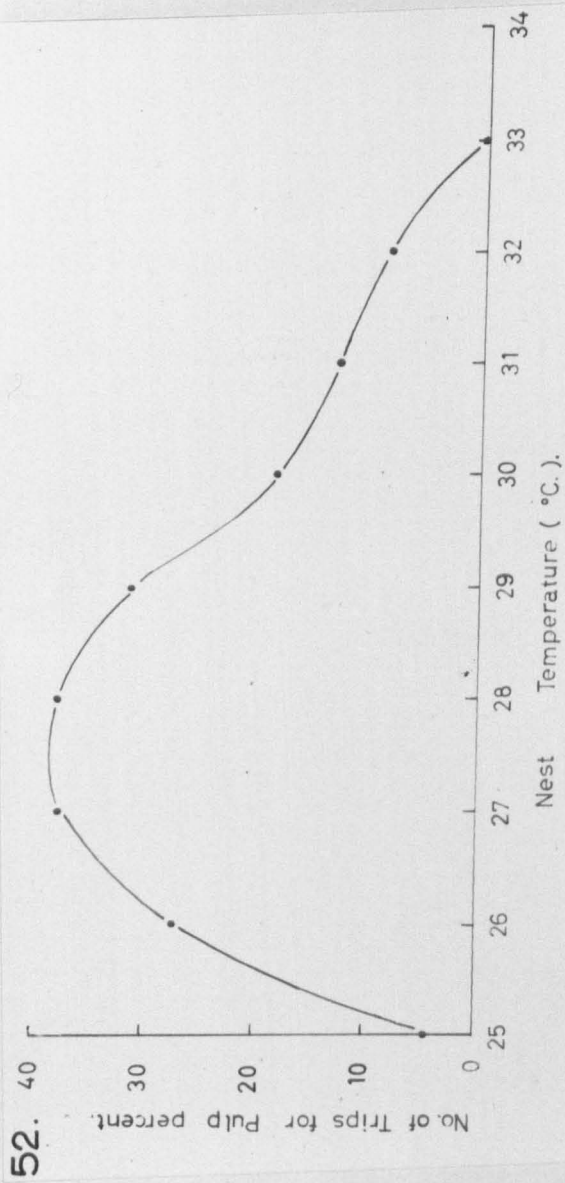


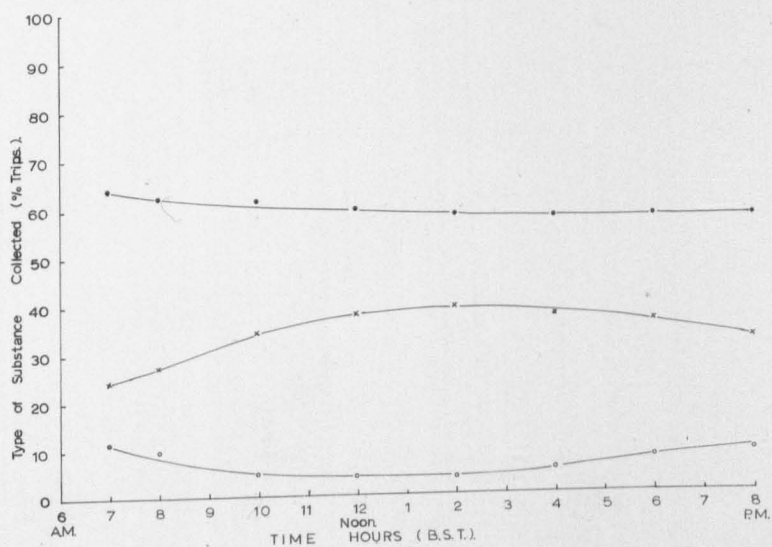
Fig. 53

Graph showing the amounts of pulp, fluid, and insect flesh collected by a nest of Vespula vulgaris kept constantly at 32°C. (the optimum nest temperature).

Fig. 54

Graph showing the amounts of pulp, fluid, and insect flesh collected by the same nest kept at 28°C.

53.



54.

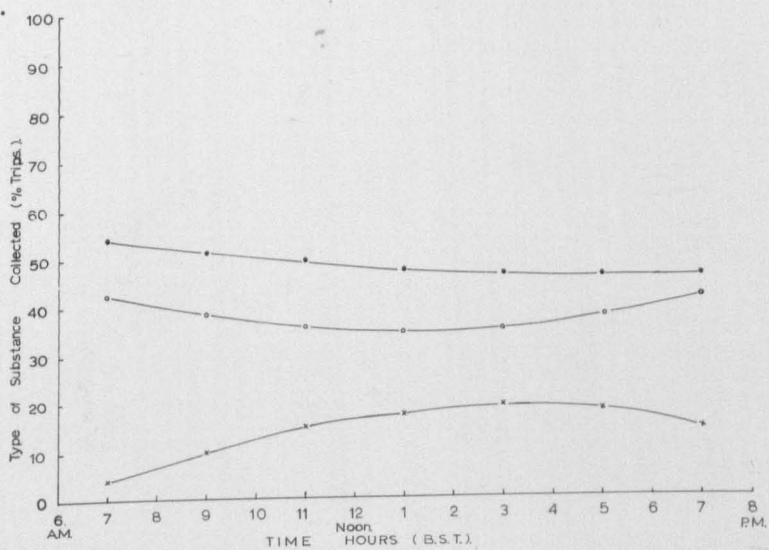


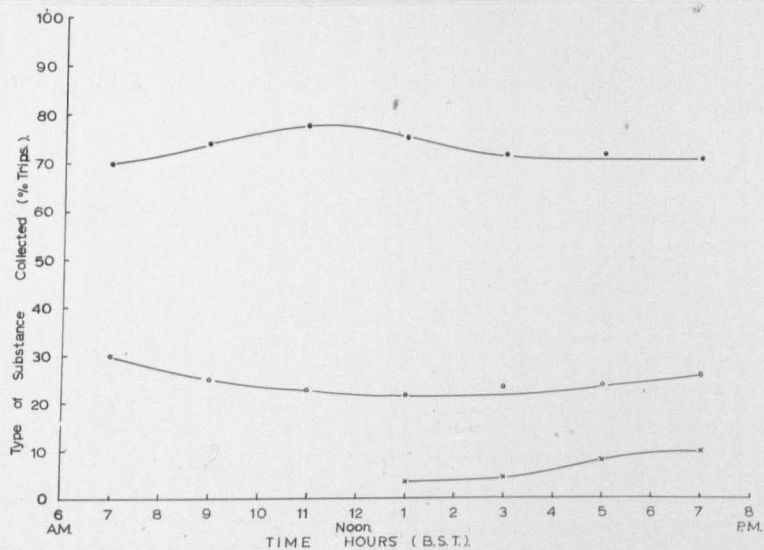
Fig. 55

Graph showing the amounts of pulp, fluid,
and insect flesh collected by the same
Vespula vulgaris nest kept at 26°C.

Fig. 56

Graph showing the amounts of pulp, fluid,
and insect flesh collected by a Vespula
vulgaris nest kept at 32°C., but with the
Relative Humidity reduced by a dehydrating
agent.

55.



56.

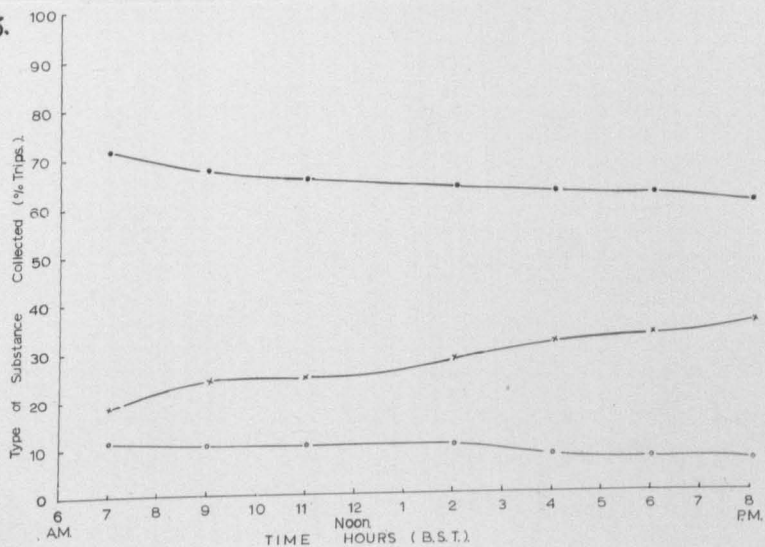


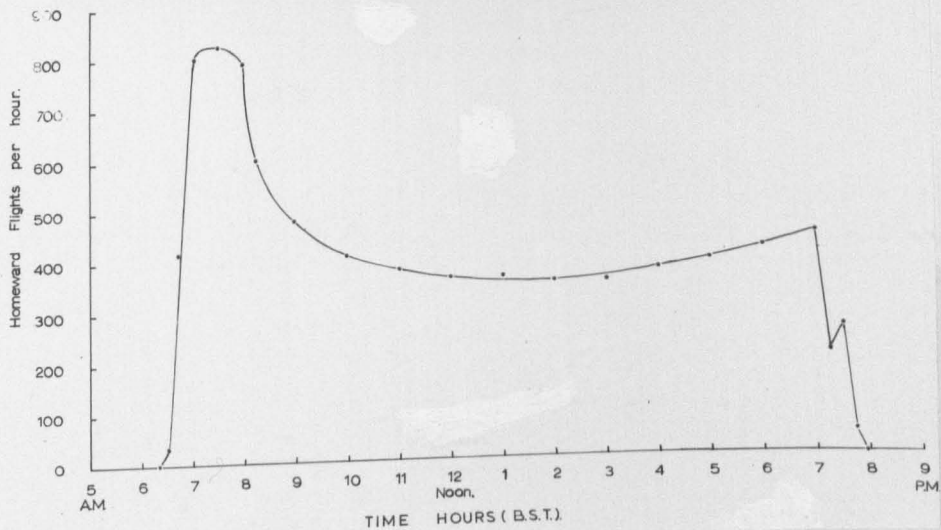
Fig. 57

Graph showing the flight activity of a
Vespula vulgaris nest on September 9th
1962, before the implantation experiment.

Fig. 58

Graph showing the relative proportions
of substances collected during the above
activity.

57.



58.

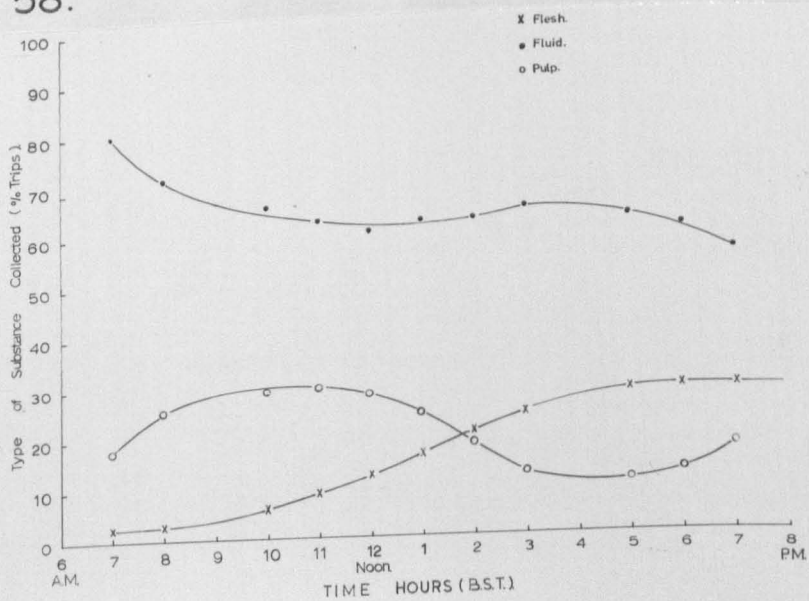


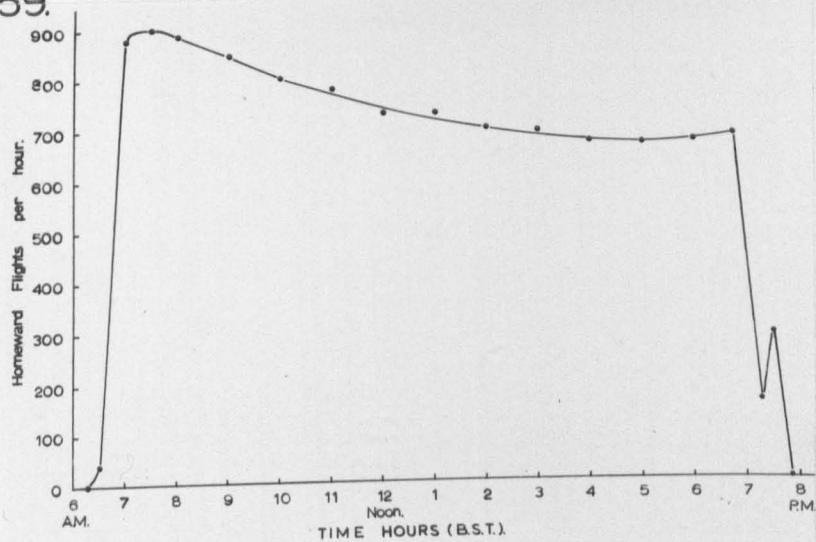
Fig. 59

Graph showing the flight activity of the Vespula vulgaris nest on September 14th, 4 days after the implantation of c.900 cells of brood (700 larvae) on September 10th.

Fig. 60

Graph showing the relative proportions of substances collected by the Vespula vulgaris nest during the above activity.

59.



60.

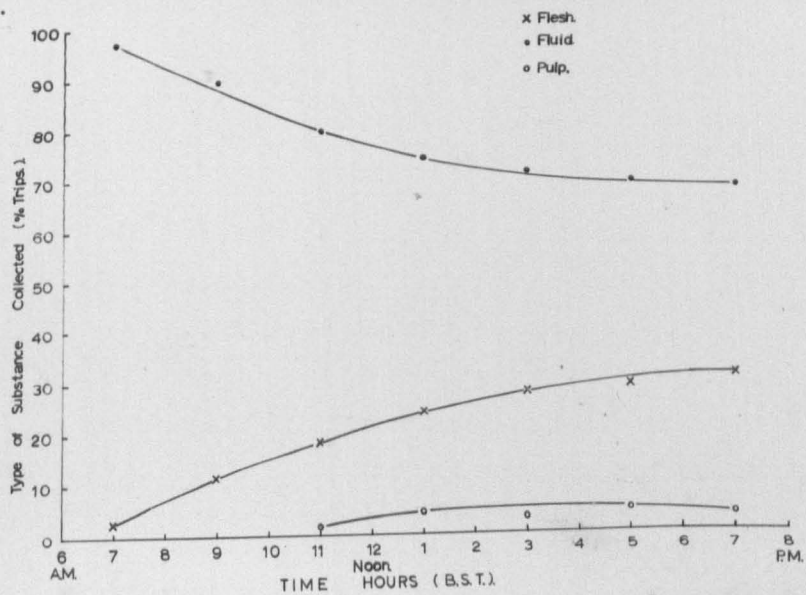


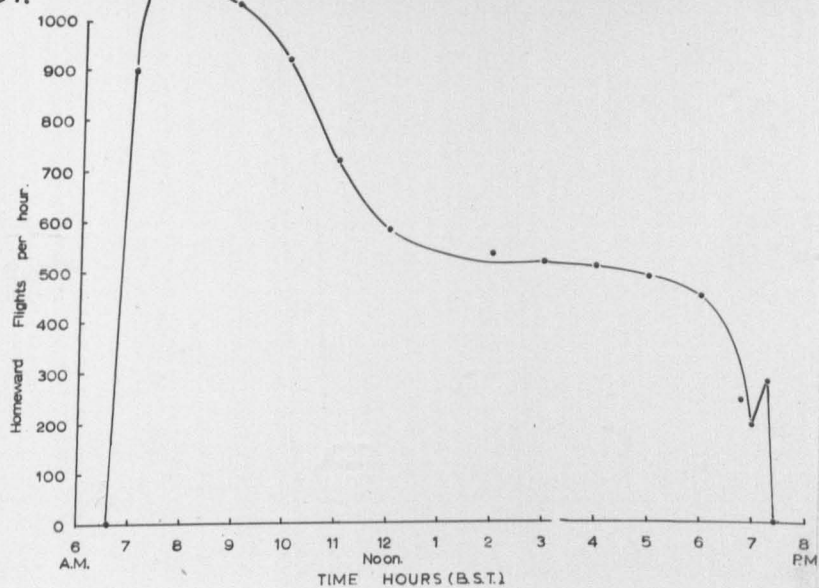
Fig. 61

Graph of the flight activity of the
Vespula vulgaris nest on September 26th,
16 days after the implantation of comb.

Fig. 62

Graph showing the relative proportions
of substances collected by the Vespula
vulgaris nest during the above activity.

61.



62.

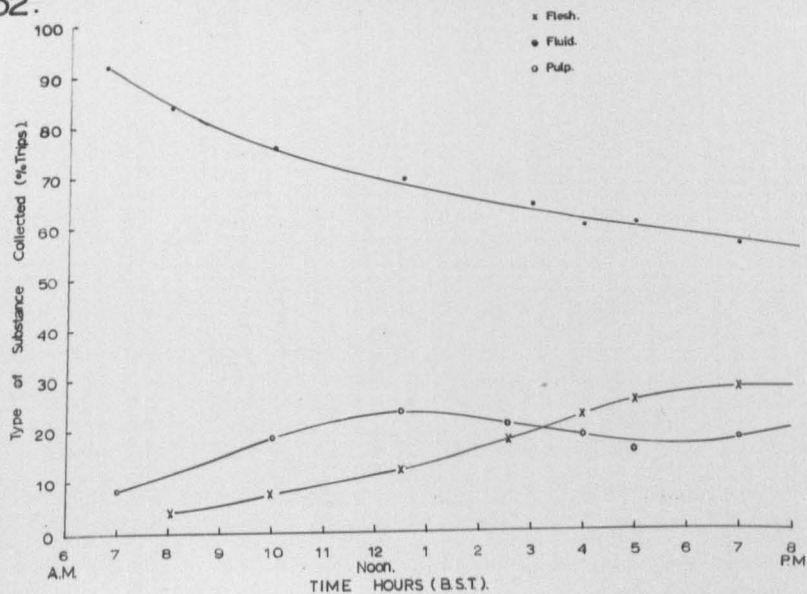


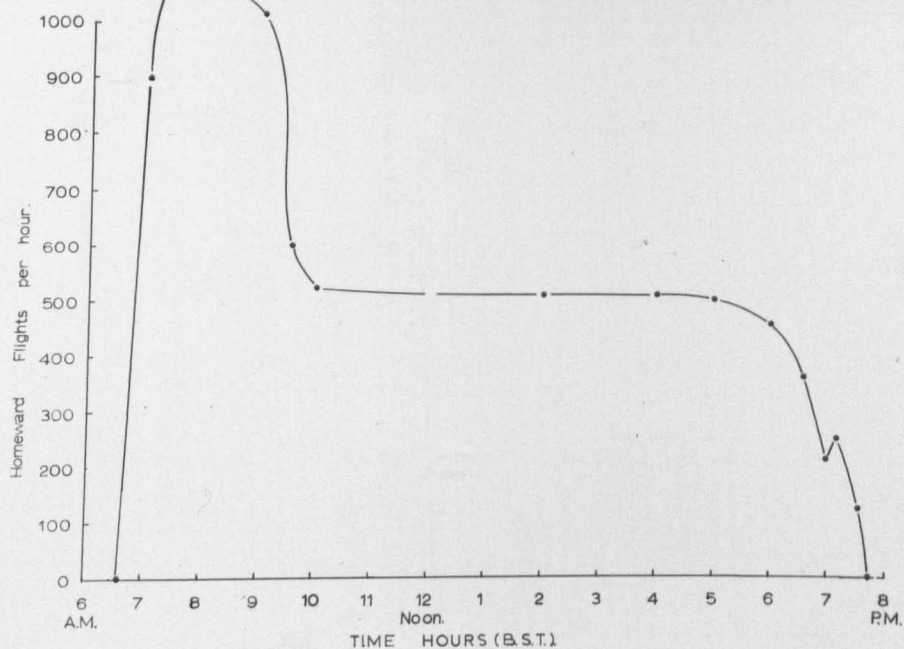
Fig. 63

Graph showing the activity of the Vespula
vulgaris nest on October 10th, 24 days
after the comb implantation

Fig. 64

Graph showing the relative proportions
of substances collected during the above
period.

63.



64.

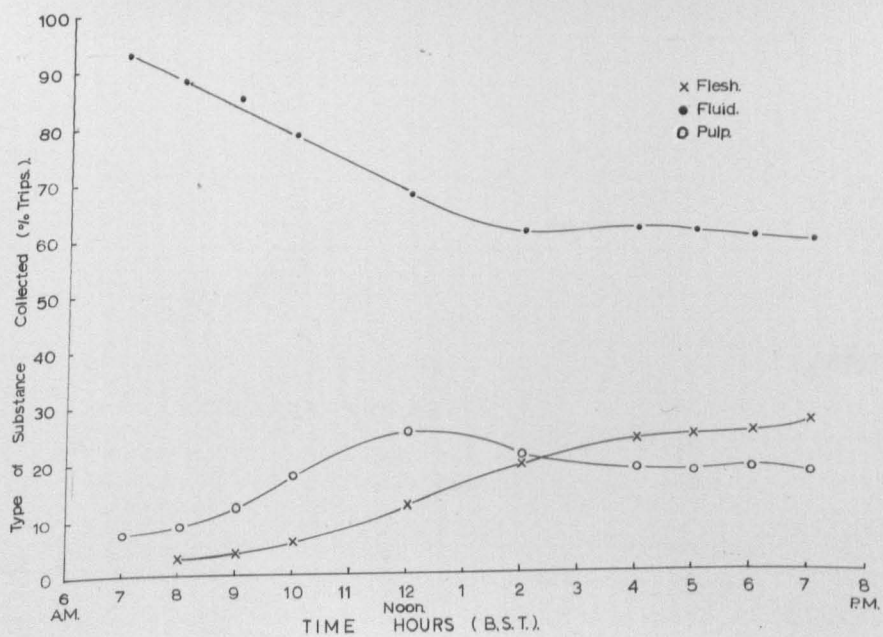


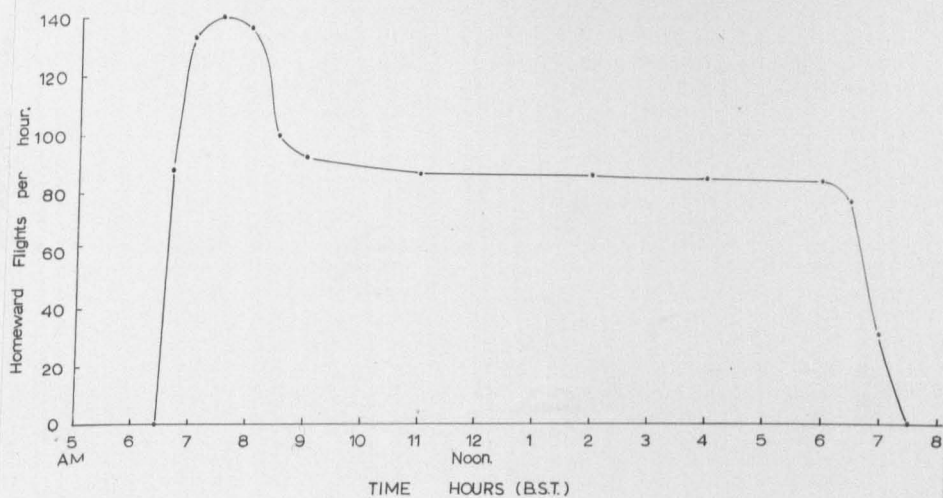
Fig. 65

Graph of the activity of a Vespula vulgaris
nest after the removal of the queen.

Fig. 66

Graph showing the relative proportions of
substances collected in the above period
of activity.

65.



66.

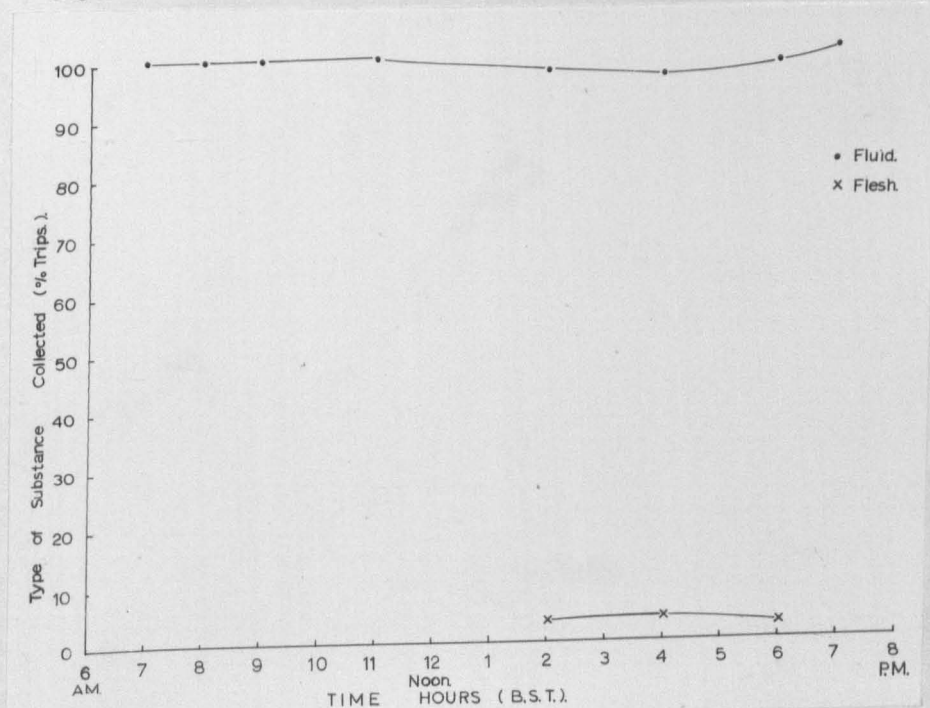


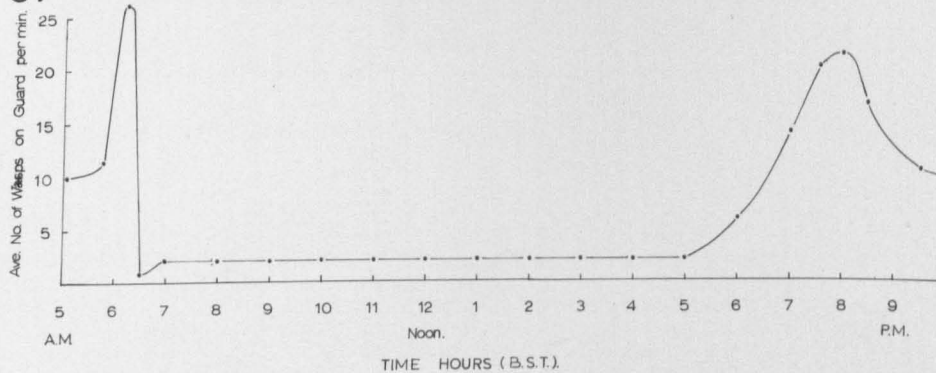
Fig. 67

Graph showing the typical guarding
activity of Vespula vulgaris on
September 2nd, 1962, a day of
continuously fine weather.

Fig. 68

Graph showing the guarding activity
of Vespula vulgaris on September 6th
1962, a day of high wind gusting to
gale force 8 (Beaufort scale)

67.



68.

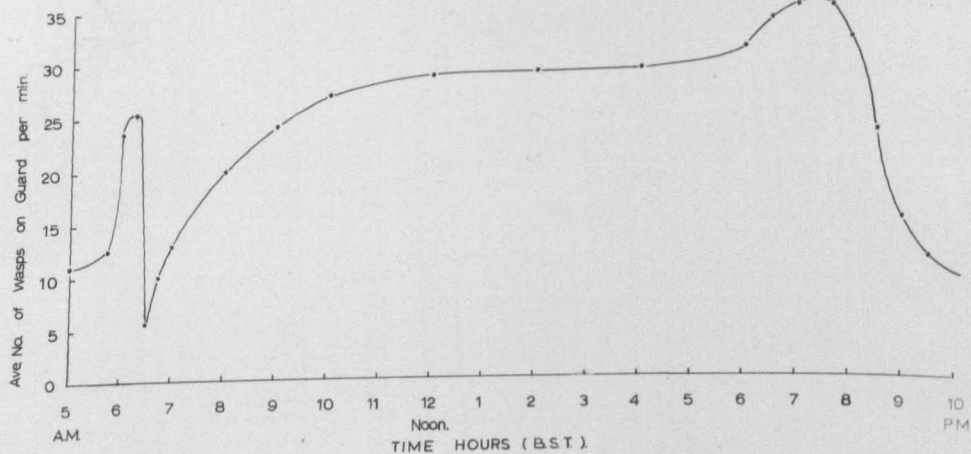


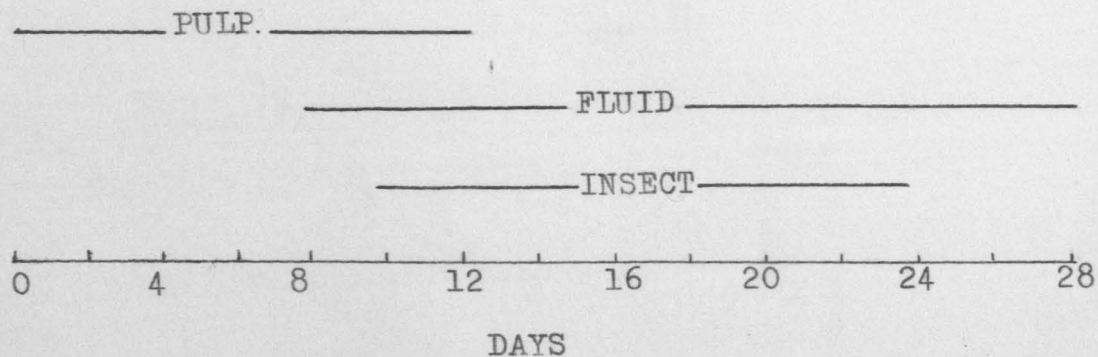
Fig. 69

Diagram showing the activity of a
Vespula vulgaris queen

Fig. 70

Diagram showing the occupations of
workers of Vespula vulgaris during
stage III, against a time scale.

69



70.

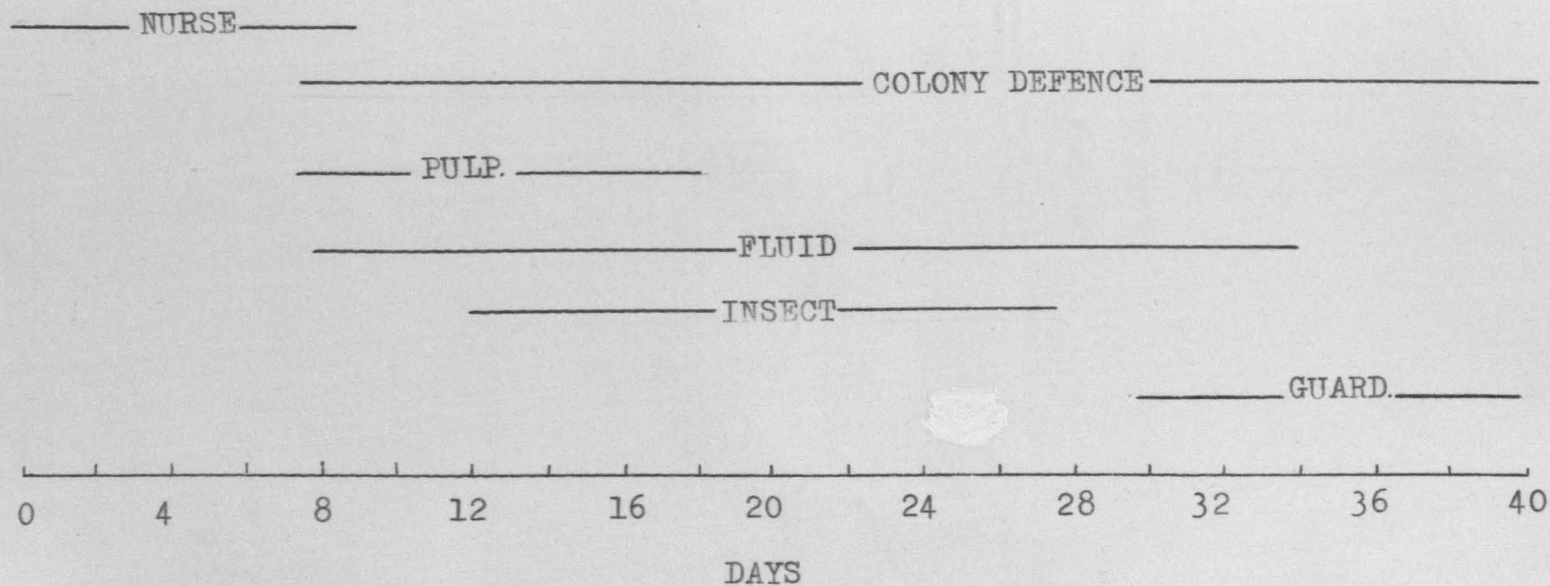


Fig. 71

Graph showing the temporal change of
foraging activities of a sample of 30
Vespula vulgaris workers during stage III.

71.

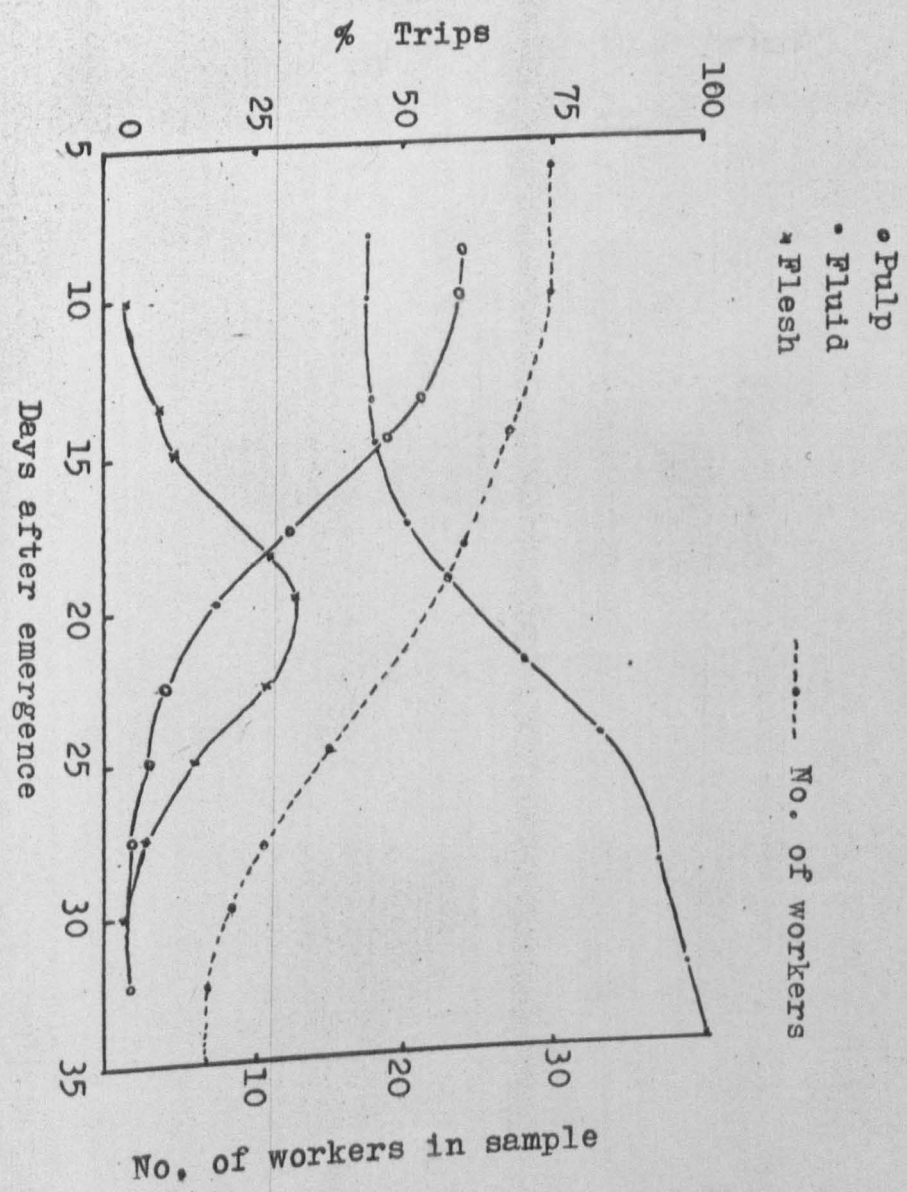


Fig. 72

Histogram showing the bimodal
distribution of wing length in
female Vespa crabro L.

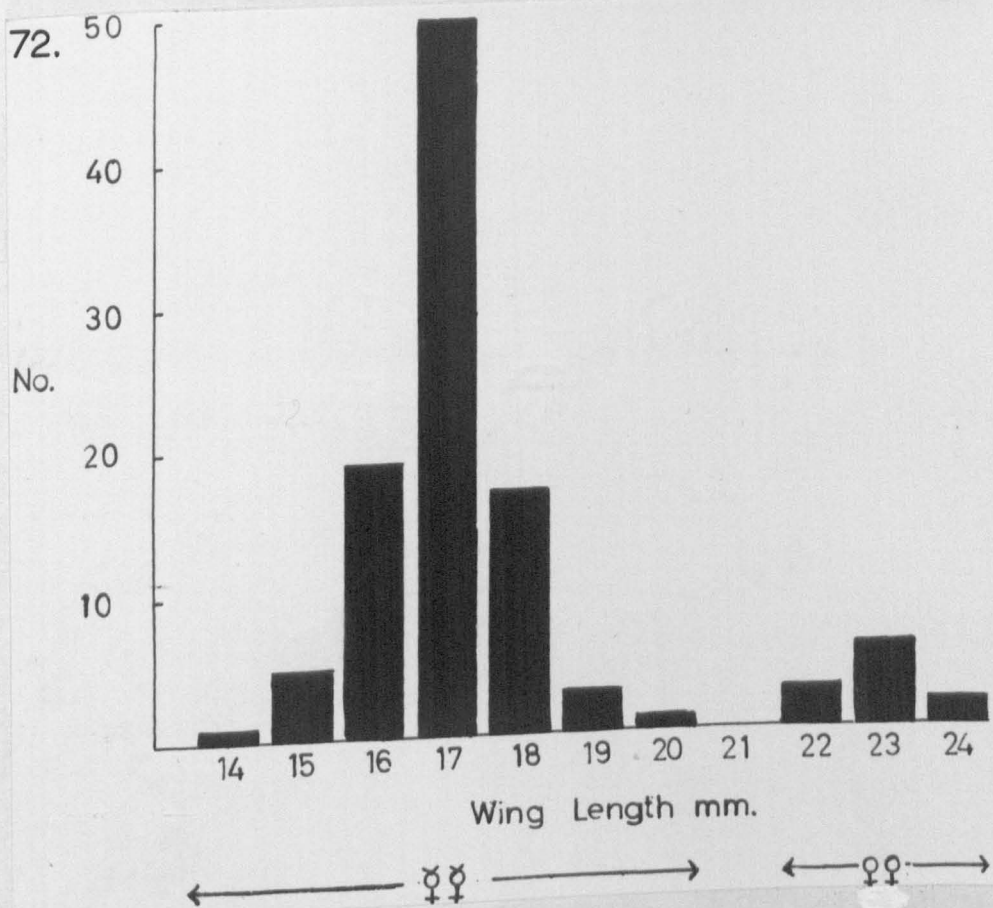


Fig. 73

Histogram showing the bimodal
distribution of wing length in
male Vespa crabro L.

73.

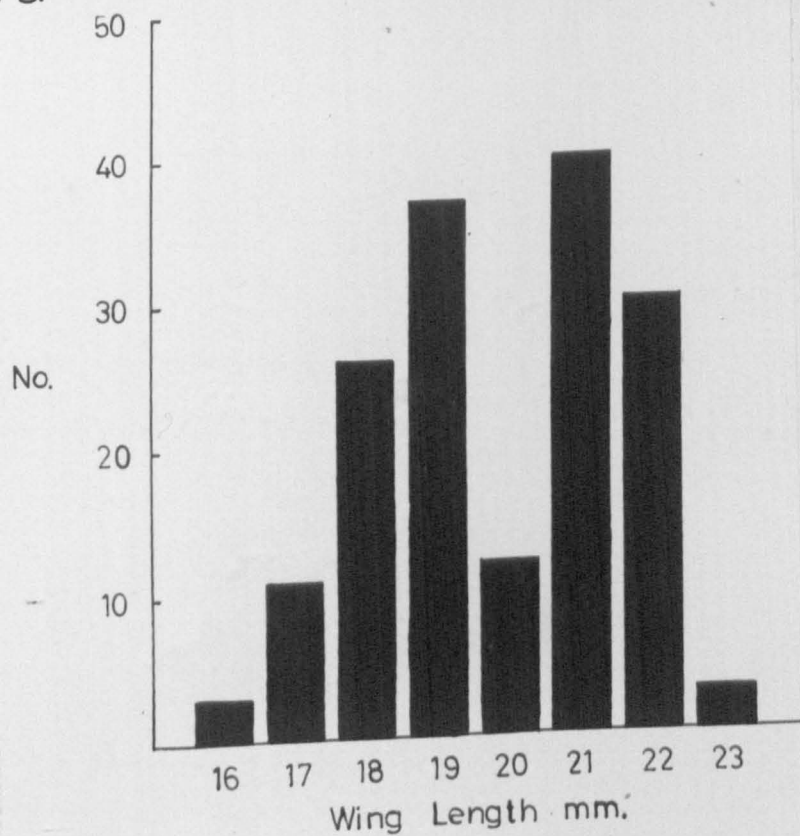


Fig. 74

A photograph of male Vespa crabro L.,
showing dimorphism.

1 - reared in queen cell

2 and 3 - reared in worker cells

74.



Fig. 75

Graph showing the weights of the
different instars of queen and worker
larvae of Vespula vulgaris L.

75.

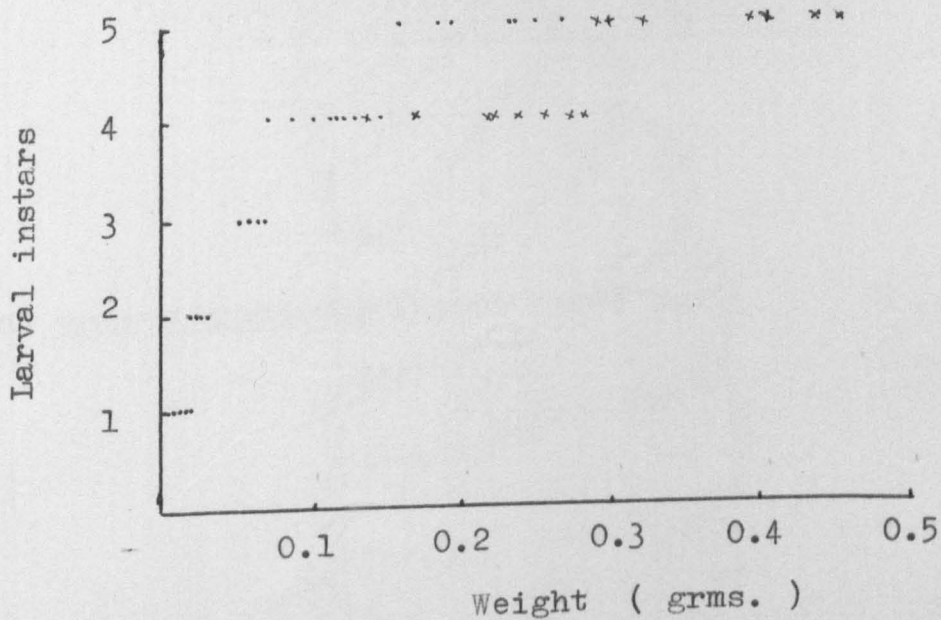
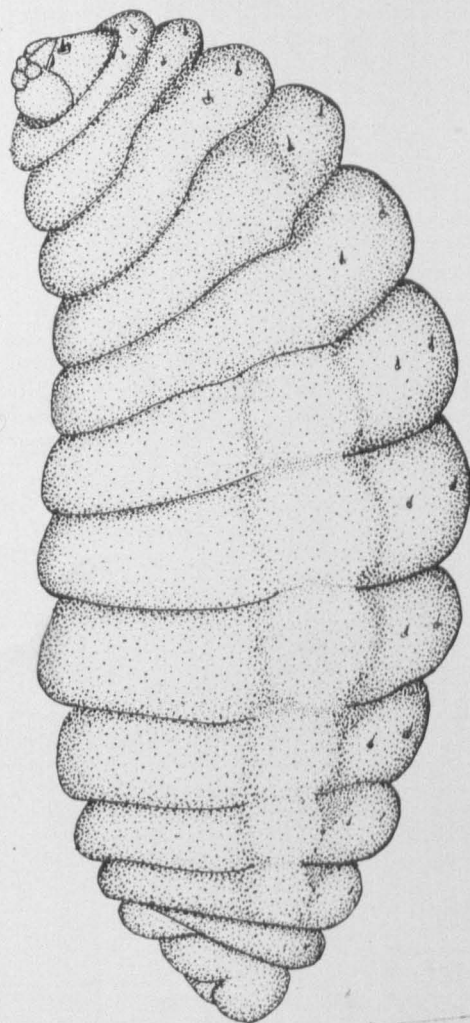


Fig. 76

Final instar larva of Sphecophaga vesparum Curt.

76.



1mm.

Fig. 77

Cocoon of Sphecophaga vesparum Curt.

- i) cell wall
- ii) } cocoon wall
- iii) }
- iv) pupa

77.

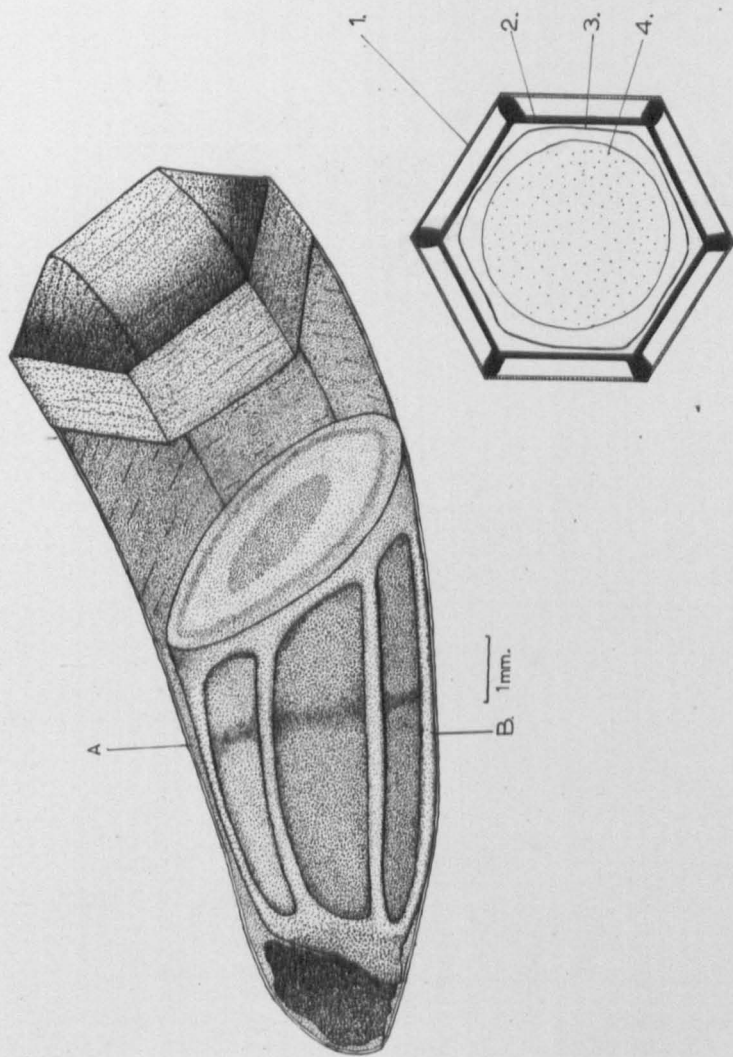


Fig. 78

Cocoon of Sphecophaga thuringiaca Schm.

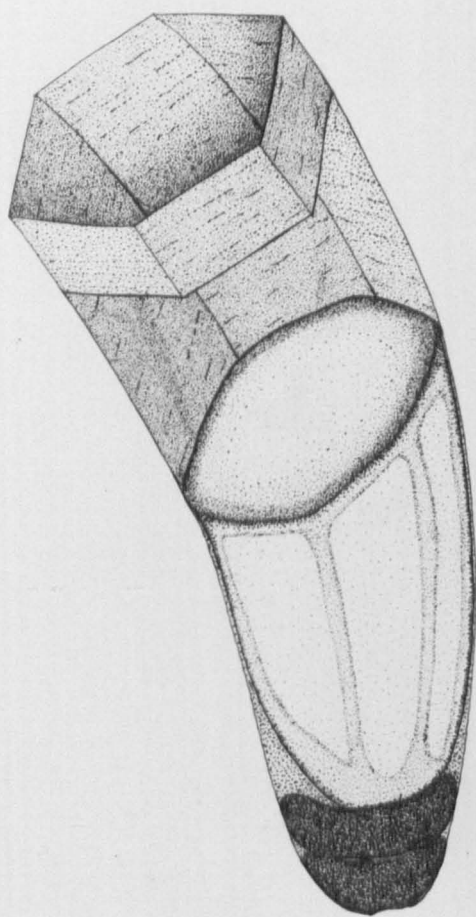
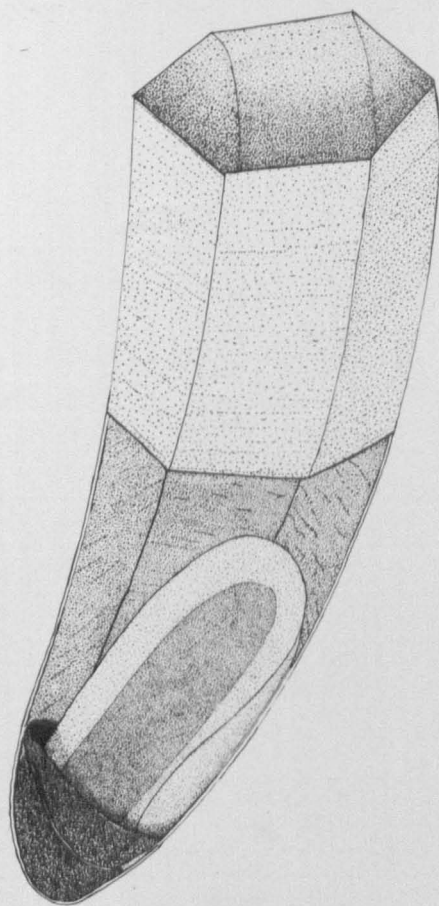


Fig. 79

Cocoon of Sphecophaga^{sp?}vesparum Curt.
h

79.

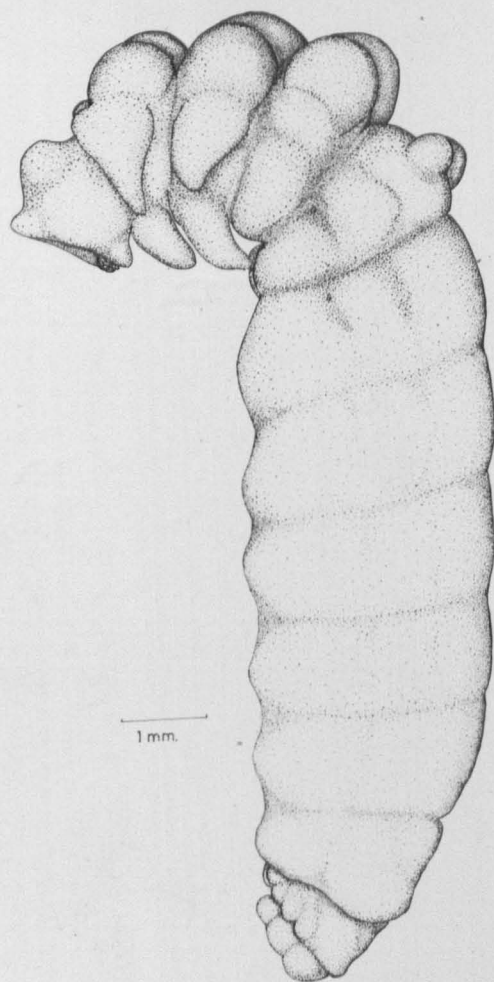


1 mm.

Fig. 80

Larva of Metoecus paradoxus

80.



APPENDIX TABLE 1

Population counts in 21 wasp nests

Nest No.	Foraging Rate Trips/hr	No. of Workers:	No. of Larvae.	No. of Pupae.	No. of Cells.
1	10	5	15	9	29
2	50	26	120	34	120
3	90	56	220	78	298
4	365	220	800	276	1076
5	620	550	1200	795	2070
6	780	556	1740	557	2300
7	675	670	1330	600	2190
8	1070	870	2200	645	3195
9	1000	910	1960	780	2800
10	956	980	1900	812	3010
11	1160	1200	3200	1160	4350
12	1350	1410	3250	1600	4800
13	1380	1550	2960	1615	4575
14	1380	1740	3000	1230	4230
15	1620	1860	3600	1475	5170
16	1630	2050	3800	1925	5825
17	1760	2410	3950	1840	5790
18	1690	2630	4200	1860	6075
19	2000	3020	4400	1730	6330
20	2020	3200	4600	1885	6600
21	2100	3600	5000	1840	7010

APPENDIX TABLE II

Population counts of wasp nests after the initiation of queen cells. In the columns headed "No. of larvae" and "No. of pupae", the lower figure in each set refers to queen brood and the upper set to the worker and male brood.

Nest No.	Foraging Rate Trips/hr	No. of Workers.	No. of Larvae.	No. of Pupae.	No. of Cells.
Q1	2400	2500	5160 15	1670 —	7320
Q2	2680	2620	5280 3	2025 —	7430
Q3	3040	2700	6000 115	2100 —	8300
Q4	3000	2620	6020 230	1875 24	8150
Q5	2860	3020	4790 150	1410 47	6400
Q6	2720	3140	5600 11	1830 —	9970
Q7	2600	2910	7390 720	2410 330	12600
Q8	2960	3180	6430 600	2370 285	10260